

# Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae)

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## Synopsis

*Acanthodactylus* is reassessed, supplementing the external features previously used with new data from the skeleton and hemipenis. The genus appears to be closely related to *Eremias* and *Mesalina* rather than to *Latastia* as was previously thought, and '*Eremias*' *guineensis* is confirmed as an *Acanthodactylus*.

It is suggested that genitalia have an enhanced propensity to 'store' evidence of shared evolutionary experience in the form of common characters among descendants, when compared with other organ systems. Such characters deserve relatively high weight in assessing relationships. However, not all genital characters can be interpreted in this way for some seem likely to have evolved as physical isolating mechanisms between similar species and, in such cases, closely related forms may have radically different genitalia. Differences of this kind, together with some osteological features, have proved important in establishing the species status of several forms usually regarded as subspecies or varieties. Thus the four subspecies of *A. cantoris* are now accorded full species status as *A. cantoris*, *A. blanfordii*, *A. schmidtii* and *A. arabicus* and a similar upgrading may well be appropriate for two taxa usually subsumed in *A. tristrami*: *A. (t.) tristrami* and *A. (t.) orientalis*. Within the *A. pardalis* complex, *A. pardalis*, *A. maculatus* and *A. spinicauda* are regarded as separate species and the form listed by

Boulenger (1921) as var. *bedriagai* is treated as a subspecies of *A. pardalis*; a similar un-named West Moroccan population is also assigned to this species. Recently available material makes it probable that *A. grandis* and *A. fraseri* are closely related and perhaps allocatable to the same highly variable species. Within the *A. scutellatus* group the following taxa recognized by Bons and Girot (1962) are assigned to *A. scutellatus* itself: *A. s. scutellatus*, *A. s. audouini*, *A. s. hardyi*, *A. i. inornatus* and *A. dumerilii*. *A. longipes* is retained as a separate species and the same status is given to *A. aureus* which Bons and Girot regarded as a subspecies of *A. inornatus*. Geographical variation requires considerable further study in a number of taxa including the *A. grandis* complex, *A. boskianus* and the *A. scutellatus* group but a number of currently recognized subspecies are invalid such as *A. tristrami iracensis* Schmidt, 1939 (= *A. (t.) orientalis*), *A. pardalis latastii* (= *A. maculatus*) and probably several of the forms in the *A. scutellatus* group.

An attempt has been made to estimate a phylogeny for the species of *Acanthodactylus*, although considerable character conflict exists.

## Introduction

The lacertid lizard genus *Acanthodactylus* Wiegmann, 1834 contains about 26 species. It occurs from Spain and Portugal across the Sahara desert and its periphery to the Red Sea, over most of Arabia and as far north as Cyprus and the Syrian-Turkish border; it also extends through Iraq, south and east Iran, south Afghanistan, Pakistan and northwest India. All its members are quite small, maximum body sizes of populations varying from about 52 mm to around 105 mm from snout to vent. They are diurnal and essentially ground-dwelling lizards usually found in relatively flat, often sandy situations and occurring in a wide variety of dry habitats which usually have at least some vegetation and range from open woodland to the borders of quite severe desert. Substrates occupied vary from quite hard loess and clay to aeolian sand. All species appear to be mainly active hunters and feed largely on small invertebrates including ants. Body temperatures of normally active animals are usually in the range 36° to 41° C (personal observations; Duvdevani & Borut, 1974a). Like most open-country lizards, *Acanthodactylus* species are probably very prone to bird predation and are also taken by other vertebrates such as snakes and monitor lizards (*Varanus*). Predator avoidance seems to depend largely on crypsis (colour match with substrate is often very good), fleeing, tail autotomy and the use of burrows. All species are oviparous and usual clutch size varies from two to about seven eggs, females in many populations appearing to produce more than one clutch annually. The majority of forms seem to mature within a year of hatching although some, like *A. erythrurus* in Spain and Portugal, may take two seasons.

The most detailed synopsis of the genus to date is that of Boulenger (1921) which although inevitably to some extent out dated, remains extremely useful, providing detailed descriptions of many forms. However, the amount of material available for study has increased massively over the past fifty years. In particular, specimens from many areas previously unsampled, such as much of the Sahara desert and Arabia, have been obtained. Furthermore, both Boulenger and subsequent workers have depended almost entirely on external characters. As there are reasons for believing that these on their own can be misleading when judging lacertid relationships (see for example Arnold, 1973) it seems worthwhile to increase the range of characters considered and, in the present paper, osteology and the structure of the hemipenis are taken into account.

What follows is not a formal revision but an overview of *Acanthodactylus* is given paying especial attention to the objective reality of the genus, species boundaries and, so far as they can be judged, inter-relationships of its members. Although the results presented here differ considerably from previously held opinions, the genus still requires a more detailed appraisal based on the large but scattered collections available in continental Europe and North America.

In this paper, the methods of phylogeny estimation employed are those discussed by Arnold (1981a). They depend largely but not entirely on Hennig's (1950, 1966) precept that joint possession of a derived character state is *prima facie* evidence of relationship. The word relationship is used in its genealogical sense: two species are more closely related to each other than to a third if they share a common ancestor not shared by that form. The following terms coined by Hennig are used, together with the adjectives derived from them: *apomorphy*—a derived character state; *synapomorphy*—a derived character state shared by two or more species and possibly indicating their relationship to each other; *plesiomorphy*—a primitive character state; *symplesiomorphy*—a primitive character state shared by two or more species, it does not indicate their relationship. *Monophyletic* and *holophyletic* are used in the sense of Ashlock (1974).

### Abbreviations used

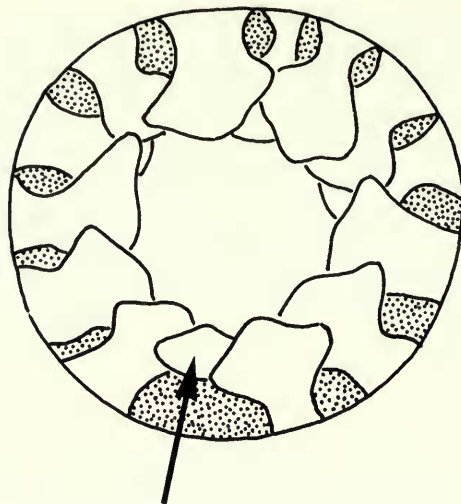
BM(NH)—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; CM—Carnegie Museum, Pittsburgh; EBD—Estación Biológica de Doñana, Seville); INHM—Iraq Natural History Museum, Baghdad; JUM—Jordan University Museum; MCZ—Museum of Comparative Zoology, Harvard; NMW—Naturhistorisches Museum, Vienna; RSM—Royal Scottish Museum; USNM—United States National Museum, Washington.

### The reality of the genus *Acanthodactylus*

On the basis of external features, Boulenger (1918a) described the genus *Acanthodactylus* as 'un des plus naturels et des plus nettement délimités de la famille des Lacertides'. Examination of skeletal and hemipenial characters provides additional support for Boulenger's view and *Acanthodactylus* is confirmed as a clearly defined assemblage that shows no integration into other genera. Most of its features are found in the lizard usually known as *Eremias guineensis* but it is certain that this form should really be included in *Acanthodactylus* (see p. 296). Features present in all or most species are listed below.

1. Frontal bones completely fused in adults and at least largely so in juveniles.
2. Often a fontanelle in the anterior wall of the orbit between the frontal and prefrontal bones.
3. A backwardly directed spur of jugal bone absent.
4. Parietal fontanelle present,
5. Parietal bone not projecting backwards over the supraoccipital.
6. Postorbital and postfrontal bones usually separate (fused only in *A. cantoris*).
7. Postorbital bone not filling supratemporal foramen.
8. Parietal and squamosal bones not usually in contact.
9. Pterygoid teeth present or absent (often considerable intraspecific variation).
10. Epipterygoid not usually in direct contact with pro-otic bone.
11. Fourteen scleral ossicles present in each eye.
12. Scleral ossicle number 14 (following numbering system of Gugg, 1939) lacks a radially directed peripheral section (see Fig. 1).
13. Number of presacral vertebrae ranges from 23 to 27, in most cases 23–26.
14. In the post-thoracic series of free dorsal ribs, the longer anterior ribs are fewer than the shorter posterior ones.
15. Ribs on last presacral vertebra very reduced or absent.

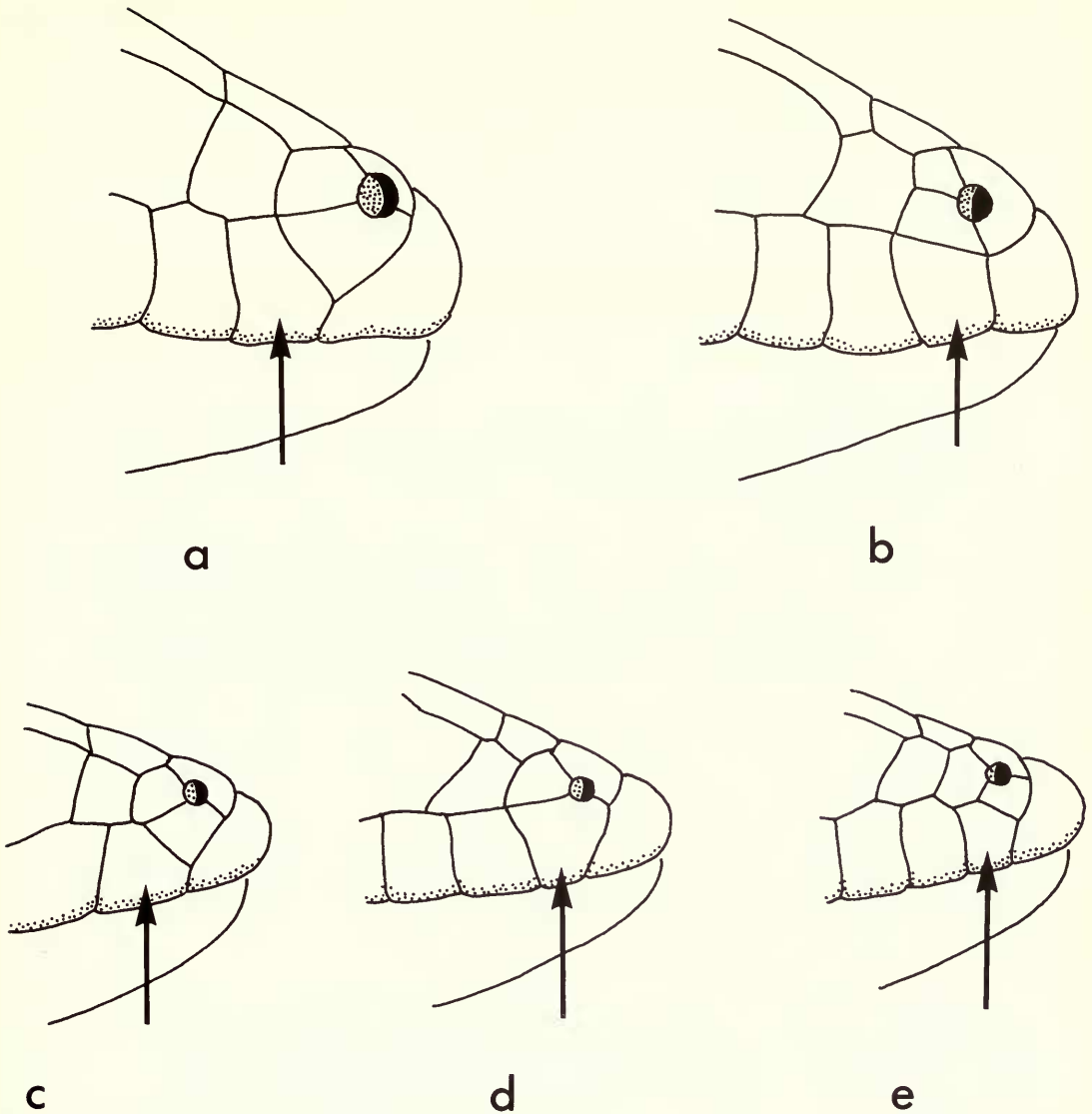




**Fig. 1** Scleral ossicles of *Acanthodactylus*; arrow indicates scleral ossicle 14 which lacks a radially directed peripheral section.

16. Sternum with a more or less heart-shaped fontanelle, which is sometimes divided into left and right sections.
17. Sternal: xiphisternal rib formula 3 : 2 or less commonly 3 : 1.
18. Clavicle expanded medially with a large fenestra in this region, so that the bone forms an uninterrupted loop.
19. Interclavicle cruciform, the lateral arms usually directed obliquely forwards.
20. Only the principal coracoid foramen present.
21. Caudal vertebrae of the C-type (Arnold, 1973: 305); that is, the most anterior autotomic vertebrae have two pairs of transverse processes, the members of the posterior one being longer and directed obliquely backwards.
22. Hemipenis and armature usually asymmetrical with medial side reduced (see p. 300).
23. Hemipenis with an armature consisting of a flat intramuscular plate, one or two clavulae and short connectors.
24. In species where the hemipenis and armature is not very reduced there may be more than four connectors.
25. Nostril closable by a valve hinging on the posterior side of the opening.
26. Nostril nearly always situated between a postnasal, an internasal and the first upper labial (not in *A. guineensis*, although the situation in this species is derivable from that found in other *Acanthodactylus*, see Fig. 2).
27. First upper labial broad above but sides converge downwards (not in *A. guineensis*; see comments about previous character).
28. Occipital scale reduced or, more usually absent.
29. A distinct collar of imbricate scales beneath neck.
30. Dorsals small and granular or larger, imbricate and keeled with rounded posterior borders.
31. Maximum number of ventral scales in a row across the belly varies from 8 to 18.
32. Toes with three longitudinal rows of scales around them and fingers with three or four rows.
33. Subdigital lamellae keeled.
34. Lateral rows of scales on the toes and sometimes fingers forming pectinations.
35. Femoral pores present.
36. Tail more or less cylindrical, longer than body.





**Fig. 2** Right nasal regions of *Eremias* and *Acanthodactylus*: (a) '*Eremias*' (= *Acanthodactylus*) *guineensis*, adult; (b) *Eremias nitida*, adult; (c) '*Eremias*' (= *Acanthodactylus*) *guineensis*, juvenile; (d) *Acanthodactylus erythrurus lineomaculatus*, juvenile; (e) *A. e. lineomaculatus*, atypical juvenile, BM 1966.430. Arrows indicate first upper labial scales.

Of these features, the following are probably derived, rather than primitive, within the Lacertidae as a whole: 1, 2, 3, 5, 7, 8, 10, 12, 15, 16, 21, 22, 24, 25, 27, 28, 31, 32, 33 and 34. Only number 27 appears to be unique to *Acanthodactylus* but 22, hemipenial asymmetry with the medial side of the organ reduced, is found elsewhere only in *Philochortus* Matschie, 1893 which, on other grounds, does not seem to be closely related. Monophyly is also suggested by (i) the great similarity between the species of *Acanthodactylus* so that they are interconnected by high levels of resemblance; (ii) possession of a unique combination of derived features even if they themselves are not unique to the genus; (iii) a coherent geographical range.

The relationship of *Acanthodactylus* to other lacertids is difficult to judge outside the

context of a comprehensive revision of the Lacertidae. Boulenger (1921) suggests that the genus is related to *Latastia* Bedriaga, 1884 but the two share only a couple of the derived features listed above, namely 1 and 33. Most derived features are shared with *Eremias* Wiegmann, 1834 (used in the restricted sense of Shcherbak, 1974, for the Palaearctic species) and *Mesalina* Gray, 1838 (used for the north African and southwest Asian species originally referred to *Eremias*—see Arnold, 1980b). *Eremias* shares 1, 2, 3, 7, 8, 14, 15, 16, 28, 32, 33 and often 25 and 34 while *Mesalina* shares 1, 2?, 3, 5, 7, 8, 10, 15, 16, 21, 33 and sometimes 28. More characters need to be examined before it can be decided which of these is likely to be the sister taxon of *Acanthodactylus* or whether this is *Eremias* plus *Mesalina*.

### Systematic position of *Eremias guineensis*

*Eremias guineensis* Boulenger, 1887a was described on the basis of a single hatchling, supposedly from 'Brass, Mouths of Niger' (Nigeria). In fact, as Schmidt (1919) has already suggested, this locality is almost certainly erroneous, or the result of accidental transportation, for all the specimens collected since have come from places far to the north of Brass in the Doka and Sudan woodland areas (vegetation classification of Rosevear, 1965) of Nigeria and Ghana (BM(NH) specimens), Niger (Pappenfuss, 1969) and Cameroon. Material from the latter country was described as a separate species, *Eremias benuensis* Monard, 1949 but Pappenfuss correctly synonymized this form with *E. guineensis*. The differences noted by Monard (p. 740) result largely from comparing adult Cameroon animals with Boulenger's description of a single juvenile, as is clearly apparent now that a number of adults are available from Nigeria and other more western localities. The ostensible differences in head and frontal scale proportions and relative head and leg lengths all result from allometric changes during growth, and the supposedly distinctive conditions of the supraocular scales, supraciliary granules and subnasal scale in *E. benuensis* can all be matched in *E. guineensis* from Nigeria. Finally the supposed difference in pattern (six white stripes on dorsum in *E. benuensis* and allegedly five in *E. guineensis* results from an error in Boulenger's description.

Boulenger placed *E. guineensis* in *Eremias* sens. lat. because it has the combination of fine dorsal scaling, keeled subdigital lamellae and nostril separated from the first upper labial scale that this author regarded as diagnostic of the genus. But he felt that this species occupied an isolated position within the assemblage and assigned it to a new subgenus, *Taenieremias* Boulenger, 1918b. This separation of *E. guineensis* from the rest of *Eremias* sens. lat. appears valid, for it differs in a number of features from the three main groups included in Boulenger's concept of the genus. It can be distinguished from *Eremias* proper (a Palaearctic assemblage) by having its postorbital and postfrontal bones unfused, by absence of a radially directed peripheral section on scleral ossicle number 14, possession of C-type caudal vertebrae, a reflectable collar and an asymmetrical hemipenis; from members of *Mesalina* by absence of a radially directed peripheral section of scleral ossicle number 14, absence of an occipital scale, possession of three rows of scales around the digits, which are pectinate, and an asymmetrical hemipenis; and from the Ethiopian species usually referred to *Eremias* and the probably related *Meroles* by C-type caudal vertebrae and an asymmetrical hemipenis which differs in detail from any found in that group. It also differs from the great majority of them in its heart-shaped sternal fontanelle and in absence of a peripheral section of scleral ossicle 14 and of an occipital scale.

On the other hand, *E. guineensis* agrees with all the features of *Acanthodactylus* listed on pp. 293–294 with the exception of the arrangement of scales around the nostril (features 26 & 27). Yet even here the situation in *E. guineensis* is not very like that found in species assigned to *Eremias* sens. lat. and in size, shape and pattern of contact with each other, the scales bear a close overall resemblance to those in *Acanthodactylus*, the only obvious difference being the presence of an extra suture in *E. guineensis* running across the area occupied by the first upper labial scale in *Acanthodactylus* to produce a smaller, nominal first upper labial and a subnasal scale that is radically different in form from that found in

members of *Eremias* sens. lat. (Fig. 2). Evidence that the *E. guineensis* condition is easily derived from that found in *Acanthodactylus* is provided by a juvenile *A. erythrurus lineomaculatus* (BM(NH) 1966.430) which, although normal in other respects, possesses an extra suture that virtually duplicates the condition found in *E. guineensis* (Fig. 2e).

In addition to possessing the overwhelming majority of the features found in all or most *Acanthodactylus*, *E. guineensis* bears a more detailed resemblance to *A. boueti* of north Dahomy and Ghana and to *A. erythrurus* and *A. savignyi* of northwestern Africa (p. 318). Given this degree of similarity, it seems best to transfer *E. guineensis* to *Acanthodactylus*, as suggested elsewhere (Arnold, 1980b).

### Characters varying within *Acanthodactylus*

The following features may vary between species of *Acanthodactylus* and are therefore potentially useful in defining species and in attempting to work out their inter-relationships. Species names mentioned in the course of description are used in the senses employed subsequently in this paper. A summary of many of the features is given in Tables 8 and 9.

#### Osteological characters

*Shape of the premaxillary region* (Fig. 3).

In many *Acanthodactylus* the outer edge of the premaxilla (viewed from above or below) is smoothly continuous with those of the maxillae, but in some species this bone is abruptly narrowed and there may be a slight constriction where its lateral surfaces meet the maxillae.



Fig. 3 Premaxillary regions of *Acanthodactylus* skulls from beneath: (left) *A. erythrurus*—outer edge of maxilla and premaxilla smoothly continuous; (centre) *A. schmidtii* premaxilla abruptly narrowed; (right) *A. scutellatus*—premaxilla abruptly narrowed and premaxillary teeth reduced to five. pm—premaxilla m—maxilla.

This condition is strongly developed in *A. blanfordii*, *A. schmidtii*, *A. arabicus*, *A. gongrorhynchatus*, *A. haasi*, *A. masirae* and especially the members of the *A. scutellatus* group: it is at least indicated in many *A. boskianus*, *A. cantoris* and *A. opheodurus*. A smooth lateral border to the anterior part of the skull is the usual condition in lacertids and the narrowing found in some *Acanthodactylus* is almost certainly apomorphic. It is best developed in species habitually living on soft sand. These forms usually have very acutely pointed snouts and at least some probe the sand when hunting, perhaps in response to tactile or aural cues originating from hidden invertebrates. Narrowing of the premaxilla may be related to producing the acuminate snout-tip necessary for this activity.

#### *Number of premaxillary teeth.*

The usual number of premaxillary teeth in most *Acanthodactylus* species is seven with occasional individual variation to six or eight. The three specimens of *A. boueti* checked are singular in apparently having nine premaxillary teeth while many members of the *A.*



*scutellatus* group have only five; this is true of the great majority of *A. scutellatus* and *A. longipes* examined but of only a few *A. aureus* (see p. 328). As the number of premaxillary teeth in most lacertids is about seven to nine, five seems likely to be an apomorphic condition within *Acanthodactylus*. Its development may well be connected with the narrowness of the premaxilla in these forms.

#### *Postorbital and postfrontal bones.*

These elements are separate in nearly all *Acanthodactylus* but they are fused in *A. cantoris*, even juvenile ones.

#### *Number of presacral vertebrae.*

There are from 23 to 27 vertebrae between the skull and the sacrum in *Acanthodactylus*. The interspecific variation encountered during this study is set out in Table 1. From this it will be seen that, in most species, males usually have more presacral vertebrae than females, the average difference in vertebral number between them varying from about 0.66 to 1.23. The main exceptions to this are *A. pardalis bedriagai* and members of the *A. scutellatus* group where average sexual differences are very small, ranging from -0.07 to 0.28. Although most populations of *A. schmidtii* show sexual differentiation in count, this is very reduced in populations from the United Arab Emirates, eastern Arabia. In the majority of species, there are 24 presacral vertebrae in most males and 25 in most females, but counts are higher in *A. (t.) tristrami*, *A. (t.) orientalis*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti* and *A. guineensis*: here males typically have about 25 presacral vertebrae against usually 26 or even 27 in females. *A. pardalis bedriagai* generally has 26 vertebrae in both sexes while in male and female *A. schmidtii* from the United Arab Emirates, *A. scutellatus* and *A. aureus* average counts approach 24; the average is even lower in *A. longipes* and in some parts of its range may be around 23.

Nearly all other lacertids show marked sexual variation in vertebral number, so its reduction is likely to be apomorphic. Counts of 23 in males and 23 or 24 in females are at the lower limit for lacertids as a whole and may well be derived conditions. Other counts are well within the normal range for the family but the higher ones, 25 in males, 26 or 27 in females, may possibly also be apomorphic as they commonly occur only in a minority of forms which on other grounds may be closely related.

In general, species with high presacral vertebral counts are found in relatively mesic habitats while those with low vertebral numbers occur in drier, more open places with sparser vegetation. It may be that the former habitat type requires more body flexion in passing through plant cover and more vertebrae facilitate this. Certainly in lacertids as a whole there is a distinct if imprecise correlation between vertebral number and habitat structure.

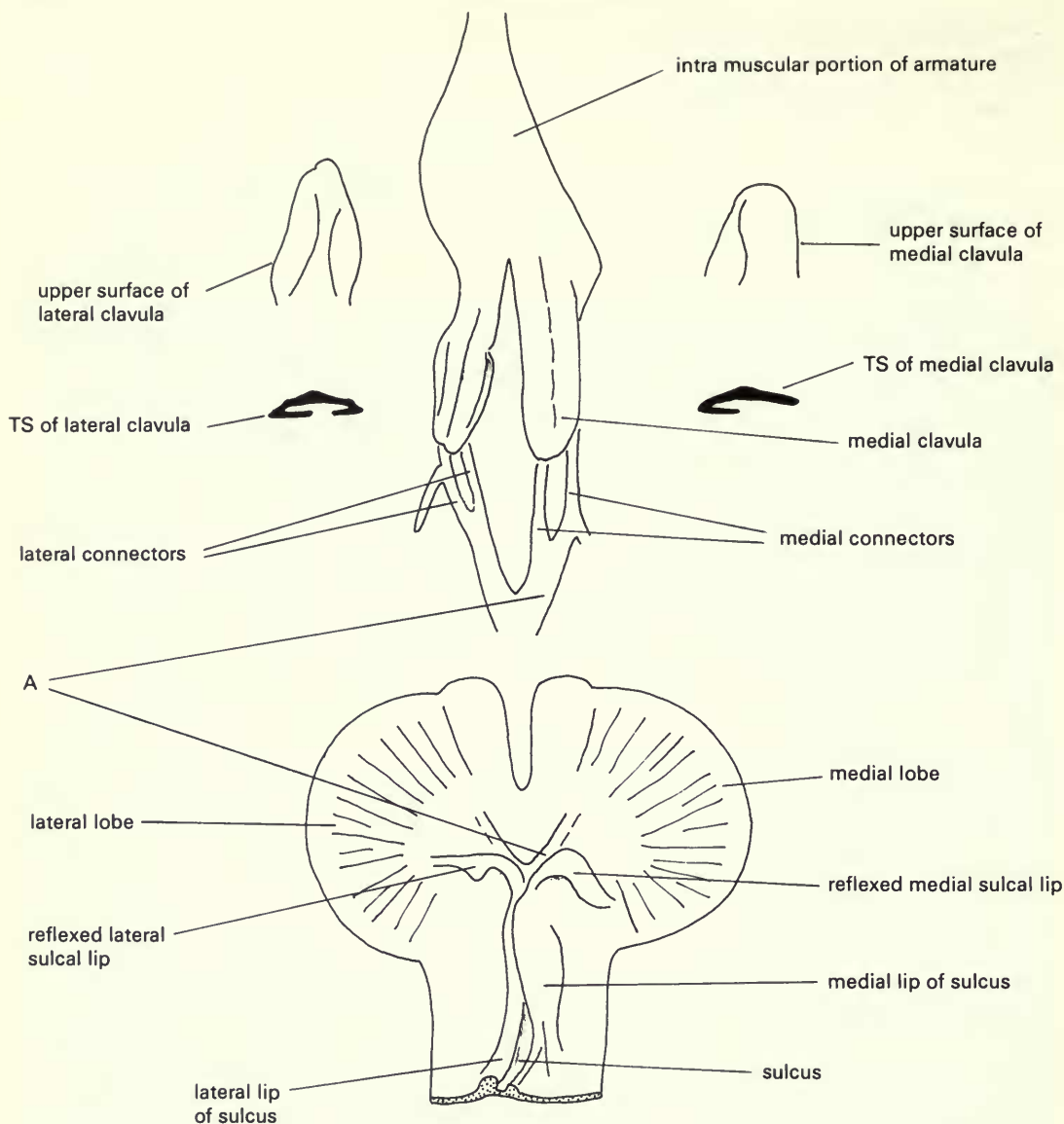
The selective pressures that cause loss of sexual differentiation in vertebral number are obscure. Possibly the difference in average count found in most lacertids reflect sex-correlated difference in microhabitat, males might, for instance, spend more time in open situations than females. If this were so, uniformity of vertebral number might result from lack of such microhabitat differences, something that seems quite probable in the relatively uniform, open environments occupied by *A. schmidtii* and the *A. scutellatus* group. Another possibility is that the extra vertebrae of most female lacertids increase the length of the body cavity for carriage of eggs and that loss of sexual differentiation is a correlate of small clutch mass. However, although egg number in the *A. scutellatus* group at least is quite small ( $n = 2$  or 3) there is no clear evidence that a clutch occupies a smaller proportion of the body cavity than in most other species of *Acanthodactylus*.

#### *Sternal ribs.*

In the great majority of *Acanthodactylus* species the usual sternal rib formula is 3 : 2, that is three pairs of ribs attach directly to the sternum and two to the xiphisternum. However, in nearly all of these, the fifth sternal rib is interrupted on at least one side in a minority of individuals, albeit often only briefly. In contrast, interruption is the commoner condition in

**Table 1** *Acanthodactylus*: variation in number of presacral vertebrae and incidence of interrupted fifth sternal ribs

	Number of presacral vertebrae										Average difference between males and females	Proportion of animals in which the fifth sternal rib is interrupted
	Males					Females						
	23	24	25	26	27	23	24	25	26	27		
<i>A. micropholis</i>		2						2			1.0	2/2
<i>A. cantoris</i>		5						3			1.0	1/8
<i>A. blanfordii</i>		8	1				1	7			0.77	3/16
<i>A. schmidtii</i>												
United Arab Emirates												
Others	1	9				1	8	4			0.33	3/18
<i>A. arabicus</i>	1	6						6			1.1	1/10
<i>A. gongrorhynchatus</i>	1	8					1	7			1.1	6/14
<i>A. haasi</i>	1	1					1	1				2/3
<i>A. boskianus</i>												0/1
<i>A. schreiberei</i>	22	3				1	5	13	1		0.68	4/43
<i>A. grandis</i> complex	10						1	8	1			3/20
<i>A. (t.) tristrami</i>	9							9			1.0	5/17
<i>A. (t.) orientalis</i>		5	1						5	2	1.13	4/13
<i>A. robustus</i>		4							4			2/2
<i>A. erythrurus</i>		3						1	1	1	1.0	3/5
<i>A. savignyi</i>	1	12					1	1	9	3	1.23	5/28
<i>A. boueti</i>		8							6		1.0	
<i>A. guineensis</i>		3						1	1		1.5	
<i>A. pardalis pardalis</i>		3							6		1.0	0/9
<i>A. pardalis bedriagae</i>		7	5					11	2		0.73	20/24
<i>A. maculatus</i>		1		13					6		0.07	10/18
<i>A. spinicauda</i>	3	29	4				1	26	3		1.04	6/10
<i>A. aureus</i>		7						3			2.0	7/10
<i>A. scutellatus</i>	1	9					1	8	1		0.1	19/20
<i>A. longipes</i>	6	30					3	45	9		0.28	62/71
<i>A. ophiodurus</i>	8	3					5	2			-0.08	9/11
<i>A. felcis</i>	1	6	4				2	11	1		0.66	4/13
<i>A. masirae</i>	5	1						9			0.84	0/13
	4							2			1.0	0/5



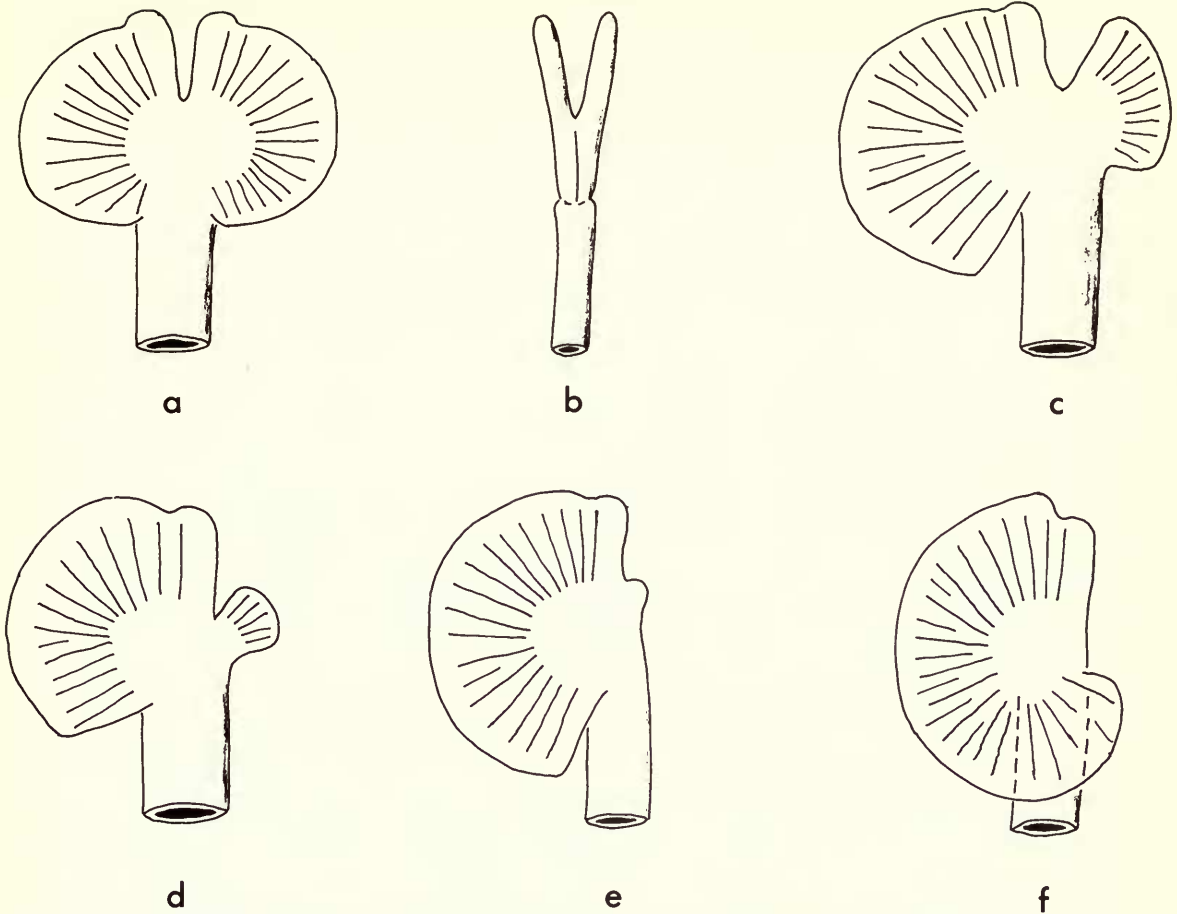
**Fig. 4** Left armature and uneverted hemipenis of *Acanthodactylus micropholis*, diagrammatic view from below, the base of the hemipenis is at the bottom of the illustration. The *m. retractor penis magnus* and ventral wall of the hemipenis have been removed, the flattened hemipenial lobes spread out and the armature disconnected: normally the points marked A coincide, with the armature lying largely above and behind the retracted hemipenis.

members of the *A. pardalis* and *A. scutellatus* groups, sometimes overwhelmingly so (Table 1.) Furthermore, the fifth sternal rib is frequently reduced to quite a small vestige.

### Hemipenial characters

Like many other lacertids, *Acanthodactylus* has a hemipenis with an armature, that is a discrete and complex supporting structure of dense connective tissue situated mainly in and around the *penis retractor magnus* muscle. Its basic anatomy and that of the lacertid





**Fig. 5** Uneverted left hemipenes of *Acanthodactylus* spp. showing variation in form and symmetry. In all except (b), the lobes are flattened and normally complexly folded, but they have been spread out for illustration. (a) lobes subequal (*A. micropholis*); (b) lobes subequal but tubular and unflattened (*A. cantoris*); (c) medial lobe somewhat reduced (*A. blanfordii*, *A. pardalis* generally similar); (d) medial lobe very small (some *A. (t.) orientalis*); (e) medial lobe minute, lateral lobe large (e.g. *A. schmidtii*); (f) medial lobe absent, lateral lobe extremely large (e.g. *A. scutellatus*).

hemipenis in general are described elsewhere (Arnold, 1973; and in press) but Fig. 4 shows the salient features in *Acanthodactylus*. A number of variations between species are described below, and are illustrated in Figs 5 and 6.

#### *Size.*

Hemipenes are small in *A. cantoris*, *A. boueti*, *A. maculatus* and *A. spinicauda*.

#### *Asymmetry in the lobes of the hemipenis.*

In many species, the two lobes are subequal in size but in others the medial lobe is reduced while the lateral one increases in size and becomes more fan-like in the uneverted organ. The amount of medial reduction varies and in some cases the medial lobe is absent or minute.

Lobes subequal: *A. micropholis*, *A. cantoris*, *A. boskianus*, *A. schreiberi*, *A. grandis* complex, *A. (t.) tristrami*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti*.

Medial lobe somewhat reduced: *A. blanfordii*.

Medial lobe more strongly reduced: *A. pardalis*, some *A. (t.) orientalis*.

Medial lobe very small: some *A. (t.) orientalis*.

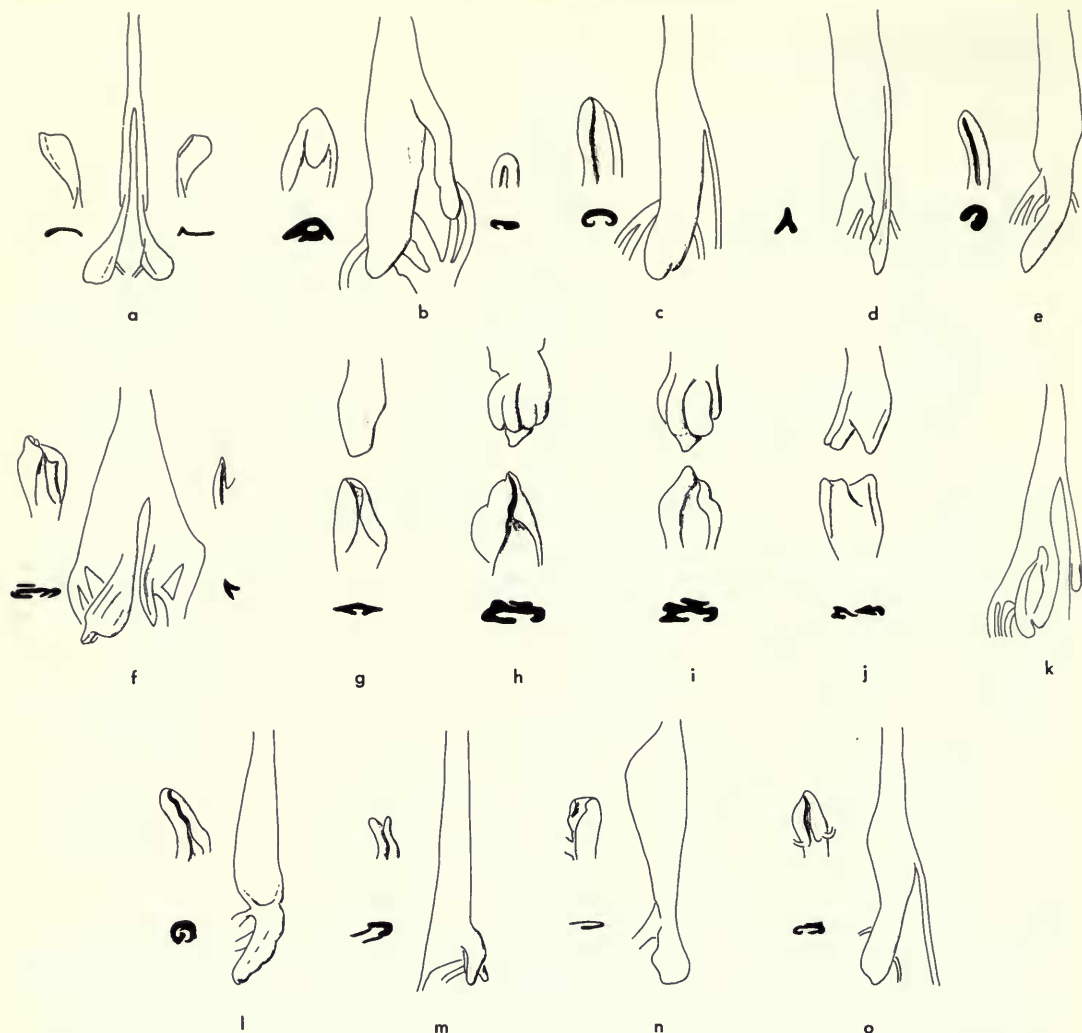


Fig. 6 Left armatures of *Acanthodactylus* species. Main views from beneath; arrangement of distal views of clavulae and of their transverse sections as in Fig. 4: (a) *A. cantoris*; (b) *A. blanfordii*; (c) *A. schmidtii*; (d) *A. arabicus*; (e) *A. gongrorhynchatus*; (f) *A. (t.) tristrami*.

A number of species have generally similar armatures to *A. (t.) tristrami* but differ mainly in the form of their lateral clavula, consequently in (g)–(j) only this is shown, ventral and dorsal views and a cross section being given: (g) *A. robustus*; (h) *A. grandis*; (i) *A. boskianus*; (j) *A. e. erythrurus*, *A. pardalis*; (k) *A. (t.) orientalis*; (l) *A. guineensis*; (m) *A. maculatus*; (n) *A. scutellatus*; (o) *A. opheodurus*.

Medial lobe minute or absent: *A. schmidtii*, *A. arabicus*, *A. gongrorhynchatus*, *A. haasi*, *A. guineensis*, *A. maculatus*, *A. spinicauda*, *A. aureus*, *A. longipes*, *A. scutellatus*, and the *A. opheodurus* group.

#### Lobe shape.

In most *Acanthodactylus*, the hemipenial lobes are flattened and fan-shaped, but complexly folded in the uneverted organ. However, in *A. cantoris* they are narrow and tubular.

#### Form of the proximal lip of the medial branch of the sulcus.

This is usually well developed and flap-like in species where the medial side of the hemi-

penis is relatively large, although it is usually reduced in forms where this is not so. *A. boskianus*, *A. schreiberi* and *A. grandis* are exceptional in having a well-developed median lobe but a weak proximal lip to the medial branch of the sulcus.

#### *Reduction of the medial side of the armature.*

In most species, the medial side of the armature is reduced in size, simpler in form than the lateral side and indeed may be entirely absent. The extent to which this reduction occurs varies and shows some correlation with reduction of the medial lobe of the hemipenis, although how precise this is varies.

Sides subequal: *A. micropholis*, some *A. cantoris*.

Medial side somewhat reduced: some *A. cantoris*, *A. boskianus*, *A. schreiberi*, *A. grandis* complex, *A. (t.) tristrami*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti*, *A. pardalis*.

Medial side more strongly reduced: *A. blanfordii*, some *A. schmidtii*, *A. (t.) orientalis*.

Medial side reduced to a thread or absent: most *A. schmidtii*, *A. arabicus*, *A. gongrorhynchatus*, *A. haasi*, *A. guineensis*, *A. maculatus*, *A. spinicauda*, *A. aureus*, *A. scutellatus*, *A. longipes*, *A. opheodurus*, *A. felcis*, *A. masirae*.

In these forms the medial branch of the sulcus is short or absent.

#### *Shape of the medial clavula.*

In species where a medial clavula is present there are two main patterns.

Clavula fairly broad, flat and blunt-tipped with at least the inner edge turned upwards: *A. micropholis*, *A. cantoris*, *A. blanfordii* and some *A. schmidtii*.

Clavula narrow and pointed with a  $\simeq$ -shaped cross section: *A. boskianus*, *A. schreiberi*, *A. grandis* complex, *A. (t.) tristrami*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti*, *A. pardalis*.

In *A. (tristrami) orientalis* the median clavula is like this or very small and flattened.

#### *Shape of lateral clavula.*

Substantial differences are found in the form of this structure.

1. Simple, flattened, often with one or both edges turned dorsally: *A. micropholis*, *A. cantoris*, some *A. schmidtii*, *A. robustus*, *A. opheodurus*, *A. felcis*, *A. masirae*.

2. Not flattened, blunt, edges folded dorsally, a central lobe on the upper surface with a proximally directed pocket: *A. blanfordii*, many *A. schmidtii*.

3. Very narrow, hollowed above: *A. arabicus*, *A. gongrorhynchatus* (*A. haasi* has a similar but shorter lateral clavula).

4. Complexly structured with multiple lobes below: *A. boskianus*, *A. schreiberi* (most medial lobe often single), *A. grandis* complex (most medial lobe often divided).

5. Complexly structured although not conspicuously lobed below, sometimes very slightly bifurcate: *A. (t.) tristrami*.

6. Complexly structured and not conspicuously lobed below but clearly bifurcate at tip: *A. (t.) orientalis*, *A. erythrurus*, *A. savignyi*, *A. boueti*, *A. pardalis*.

7. Lateral clavula simple but often bifurcate and folded to give a  $\supset$ -shaped cross section: *A. maculatus*, *A. spinicauda*.

8. Lateral clavula flattened and not bifurcate but folded to give a  $\supset$ -shaped cross section: *A. aureus*, *A. scutellatus*, *A. longipes*.

#### *Connectors.*

In some species the connectors are all relatively thin but in others the most medial one on the lateral side is usually thickened. This is found in *A. boskianus*, *A. schreiberi*, the *A. grandis* complex, *A. (t.) tristrami*, *A. (t.) orientalis*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti*, *A. guineensis*, *A. pardalis*, *A. maculatus* and *A. spinicauda*.

#### **Polarity of hemipenial features**

The only available criterion for the polarity of hemipenial features found in *Acanthodactylus* is outgroup comparison using other lacertids as the outgroup. In these, the hemipenis is



usually fairly large and symmetrical with well developed sulcal lips on both sides. Where present the armature is also typically symmetrical with simple, often flattened and rather blunt clavulae. On this basis, small size, asymmetry of the lobes, sulcal lips and armature and the development of peculiar and often complex clavulae and thickened connectors are all likely to be derived features.

### Origin of hemipenial differences

It is common in many animal groups for genital structure to vary between taxa and for at least some of its features to be considered good indicators of relationship, especially as they often correlate with characters from other organ systems. The origin of such differences and possible reasons why they should often reflect relationship are discussed at length elsewhere (Arnold, 1973; in press). It is suggested that genitals differ from other organ systems in their potential to retain changes that develop in them as a result of pleiotropic effects or transient selective forces. With most organ systems, any pleiotropically induced change is likely to result in a loss of functional efficiency. Provided this lowering of efficiency does not outweigh the original selective advantage of the genetic change concerned, the pleiotropic alteration will initially become fixed. But there will then be normalizing selection modifying the genotype so that the pleiotropic change will tend to be suppressed and the organ will return to its original state and level of efficiency. Similarly, if the organ changes in response to direct but transient selective pressure, it will tend to revert to its original condition once this pressure is relaxed.

The situation with genitalia is different since their efficiency cannot be considered in isolation but only in relation to their co-ordinated functioning with the genitals of the opposite sex. Efficiency does not depend on a particular conformation or size but on good match between the sexes. Consequently, if there were, say, a pleiotropic change affecting the male organs which reduces copulatory efficiency, there would not only be normalizing selection acting on the male genotype to bring the male organ back towards its original condition but also, simultaneously, selection acting on the female genotype to produce genital changes adapting to the pleiotropic alterations that have already taken place in the male system. This means that the two sets of genitals might return to their previous mutual efficiency without reverting to their original morphological state. The same sort of effect would be expected if transient selective forces acted directly on the genitalia themselves. Genitals are thus likely to 'store' changes, which in other organ systems would probably be eradicated. So they may be on the whole more likely to incorporate evidence of shared evolutionary experience than many other organs.

An important factor in the production of hemipenial differences in lizards, including *Acanthodactylus*, may be the development of physical isolating mechanisms when previously allopatric species come into contact. Such isolating mechanisms could reduce the loss of reproductive effort which is likely if two species interbreed. That such loss can occur is evidenced by the occasional discovery of hybrids between lacertid species (cases in *Lacerta* and its relatives are summarized by Arnold, 1973, and in *Acanthodactylus* by Mertens, 1968). Physical isolating mechanisms would be at a premium in situations where similar species with no experience of each other come into contact since, in this situation, premating isolating mechanisms may not be well developed. Interspecific mating would be reduced if considerable mismatch evolved in the shape and dimensions of the genitalia of the forms concerned. The often radically different hemipenes of otherwise similar species of *Acanthodactylus* may be examples of this, especially as they correspond in shape and size to the cloacal bursa of their own females into which the male organ is inserted. Such differences occur between forms which, on other grounds, are likely to be closely related, for instance *Acanthodactylus pardalis* and *A. maculatus* and, because they reduce the possibility of successful copulation between the forms, are *prima facie* evidence of separate species status. Some of the derived features found in the hemipenes of *Acanthodactylus* can be interpreted as contributing to such isolating mechanisms; they include not only small size but also

asymmetry of the hemipenis and armature since loss of its medial side reduces the diameter of the organ.

Although they are likely to be 'stored' beyond their period of function (presumably premating isolating mechanisms are likely to develop in the long run), changes that are probably associated with physical isolating mechanisms are not likely to be very reliable indicators of relationship. This is partly because, by their nature, they tend to produce marked differences between very similar and often closely related species. Also, means of producing incompatible genitalia are rather restricted in lizards and it is very likely that small size and asymmetry may have been produced several times. This is supported by their patchy occurrence in *Acanthodactylus*, turning up in a number of groups which on other grounds do not seem to be closely related. Furthermore these features have developed in other lacertid genera. Other hemipenial features may not be subject to such strong convergent selective forces and, as such are more likely to be good indicators of relationship for the reasons given earlier in this discussion.

### Description of the hemipenes of different species

Figures in parentheses refer to the number of individual organs examined.

*A. micropholis* (2). Lobes more or less symmetrical or medial rather reduced, sulcus bifurcate, the proximal borders of its branches formed by backwardly directed flaps; armature fairly symmetrical although one or other clavula larger than the other, clavulae rather expanded and obtusely pointed, the medial one with its inner edge turned upwards, lateral one with both edges turned upwards; often three lateral connectors and two medial ones, all narrow.

*A. cantoris* (7). Size reduced; medial lobe usually rather smaller than lateral, lobes not complexly folded, the walls often corrugated and lack regular plicae, stem of hemipenis long, sulcus bifurcate, the proximal borders of its branches formed by a soft flap in at least some cases although this is not always clear; armature symmetrical or medial side somewhat reduced, slender, the clavulae expanded and laminar, medial with inner edge turned upwards, lateral with both edges turned upwards, at least one connector on each side.

*A. blanfordii* (10). Lateral lobe large and medial one reduced, sulcus bifurcate, proximal border of lateral but not medial side formed by a backwardly directed flap; armature clearly asymmetrical, the median side reduced with a flattened clavula of which the inner edge is turned upwards, lateral clavula large and obtusely pointed, not flattened, edges turned upwards and a central lobe present on the upper side below which there is a proximally directed pocket (the lobe is least developed in southern populations), connectors as in *A. micropholis*.

*A. schmidtii* (10). Lateral lobe large and fan-shaped, medial lobe absent or minute, sulcus bifurcate but medial branch very short; medial side of armature absent or reduced to a thread in most cases; lateral clavula large, either rather pointed, slightly bifurcate or rather blunt, edges turned upwards and clavula may be rolled to some extent, a central lobe present in many cases on the upper side, below which is often a proximally directed pocket as in *A. blanfordii* but is less well developed. In one case (BM(NH) 1931.7.16.48) there is a flattened medial clavula.

*A. arabicus* (6). Essentially like *A. schmidtii* but intramuscular part of armature much narrower and lateral clavula very narrow, simple and pointed with a concavity above or the medial edge rolled upwards.

*A. gongrorhynchatus* (1). Similar to *A. arabicus* but medial edge of clavula rolled onto dorsal surface.

*A. haasi* (1). Like *A. gongrorhynchatus* but clavula shorter, broader and more dorso-ventrally flattened.

*A. (tristrami) tristrami* (3). Lobes more or less symmetrical, sulcus bifurcate, the proximal borders of its branches formed by distinct flaps; armature asymmetrical, the medial side reduced with a pointed clavula that has a  $\epsilon$ -shaped cross section; lateral clavula expanded and, when spread out, essentially flat with a very weakly bifurcate tip formed of overlapping laminae, lower surface fairly smooth but with a strap-shaped area with free edges towards outer side, upper surface with a medially directed pocket and edges rolled upwards; three lateral and two medial connectors, the more medial of the lateral ones thickened.

*A. (tristrami) orientalis* (4). Different from *A. (t.) tristrami*: lateral lobe very large and medial strongly reduced (as in Fig. 5c or d), sulcus bifurcate, proximal borders of branches formed by distinct flaps, the median one rather small; armature very asymmetrical, medial clavula quite small, either pointed with a  $\epsilon$ -shaped cross-section or blunt and flattened; lateral clavula rather similar to that of *A. (t.) tristrami* and has free strap-shaped area on lower surface but is smaller with a more bifurcate tip and no clear pockets.

*A. robustus* (2). Generally like *A. (t.) tristrami* but lateral clavula much simpler with edges turned on to dorsal surface.

*A. boskianus* (10), *A. schreiberi* (5). Generally like *A. (t.) tristrami* but proximal border of medial branch of sulcus is a relatively weak, soft fold rather than a flap; lateral clavula has similar general form but is more swollen and lobed and there is an area with free edges towards the medial side of the ventral surface; upper surface has medial edge rolled upwards and greatly swollen. In *A. schreiberi* and *A. boskianus* the median area of the ventral surface may be divided by a longitudinal cleft.

*A. erythrurus erythrurus* (3), *A. e. lineomaculatus* (3), *A. savignyi savignyi* (2), *A. s. blanci* (2). Similar to *A. (t.) tristrami* but lateral clavula usually clearly bifurcate at tip and the more median cleft in *A. (t.) tristrami*, that separates a strap shaped area with free edges in this form, is usually not clearly marked.

*A. e. belli* (6). As *A. e. erythrurus* but lateral clavula is smaller, flatter and usually simpler.

*A. boueti* (1). Size reduced; lobes subequal; armature asymmetrical, the medial side reduced with a pointed clavula that has a  $\epsilon$ -shaped cross section; lateral clavula expanded and flattened, bifurcate at tip, with lateral edge turned upwards.

*A. guineensis* (1). Lateral lobe very large, medial lobe absent, sulcus lacks medial branch, proximal border of its lateral branch formed by a backwardly directed flap; medial side of armature absent, lateral clavula superficially narrow but in fact laminar and tightly rolled, lower surface smooth but with a cleft near each margin, dorsum with a medially directed pocket; two connectors, the more medial one broad.

*A. pardalis* (20). Lateral lobe large and medial small but plicate, sulcus bifurcate, the proximal border of its branches formed by backwardly directed flaps; armature very like that of *A. erythrurus* and *A. savignyi*.

*A. maculatus* (20), *A. spinicauda* (2). Small; lateral lobe large, medial lobe absent; medial branch of sulcus very short, proximal border of lateral branch only of sulcus formed by backwardly directed flap; medial side of armature absent or reduced to a thread, lateral side narrow and clavula small but sometimes bifurcate; compared to condition in *A. pardalis*, lateral clavula has been rotated and folded to give a  $\supset$ -shaped cross section so that the bifurcation, if present, is in the vertical plane; two or three connectors, the most medial one usually thickened.

*A. aureus* (3). Lateral lobe large and fan-shaped, medial lobe absent or very small and confluent with lateral one, medial branch of sulcus absent or very short; medial side of



armature absent or reduced to a thread, lateral side broad; lateral clavula flattened but rotated sideways, as in *A. maculatus*, and folded to give a  $\supset$ -shaped cross section, with two connectors.

*A. scutellatus* (5), *A. longipes* (3). Generally similar to *A. aureus* but folded clavula usually broader and sometimes apparently only one connector present.

*A. opheodurus* (10), *A. felicis* (4), *A. masirae* (2). Lateral lobe extremely large, medial one very reduced, sulcus with relatively short medial branch, proximal border of lateral branch usually visible as a rather weak flap or fold; medial side of armature reduced to a thread or absent, lateral clavula usually flattened with the margins rolled over onto dorsal surface; lateral connectors usually two or sometimes three, slender.

### External features

These have nearly all been used by Boulenger (1918a, 1921) and subsequent authors and, until now have formed the basis of *Acanthodactylus* classification.

#### *Scales around nostrils.*

*A. guineensis* has a peculiar perinasal scale arrangement that seems to be derived from the typical *Acanthodactylus* condition, it also occurs as a rare variant in *A. erythrurus* (see p. 296).

#### *Frontonasal scale.*

This is usually intact but is frequently divided in two by a longitudinal suture in some populations of *A. erythrurus* and *A. savignyi*. The condition occurs as a rarity in a few other species.

#### *Azygos scales between prefrontals.*

One or more azygos scales between the prefrontals occurs commonly in *A. boueti*, *A. savignyi* and in some populations of *A. erythrurus*. This arrangement is also found as an uncommon variant in *A. guineensis*, *A. schreiberi* and *A. boskianus* and even more rarely in some other forms.

#### *Supraocular scales.*

There is considerable variation in the extent to which the supraocular scales roofing the orbit are fragmented in *Acanthodactylus*. 1. *A. schreiberi* has four large, more or less intact scales; this condition is approached by members of the *A. grandis* complex. 2. In the *A. cantoris*, *A. scutellatus* and *A. opheodurus* groups and in *A. gongrorhynchatus*, *A. haasi* and many *A. boskianus* there is usually an area of granules wedged between the third and fourth supraoculars and, in some cases, between the first and second too; the fourth supraocular may also be broken up, at least to some extent. *A. boskianus* from north Egypt and *A. haasi* may have the first supraocular divided into two or three sections. 3. Members of the *A. pardalis* group have the first supraocular sometimes divided into two or even three and the fourth is very fragmented. 4. In the *A. tristrami* and *A. erythrurus* groups the first supraocular is divided into at least three sections and often into many granules and this usually applies to the fourth too. 5. *A. boueti* has the first, second and third supraoculars all fragmented. There is however a significant amount of variation within taxa.

It is probable that the plesiomorphic condition is four more or less undivided supraocular scales, as this is by far the commonest state in the Lacertidae as a whole, but fragmentation seems to have occurred independently in some forms assigned to *Eremias* and in *Ichnotropis*.

#### *Subocular scale.*

A number of species have a subocular scale that extends ventrally to the edge of the mouth, separating the, in these cases, usually four anterior upper labial scales from the remainder. This condition is found in *A. (t.) tristrami*, *A. (t.) orientalis*, *A. masirae*, *A. boueti* and *A. guineensis*, in many *A. micropholis*, *A. erythrurus* and *A. savignyi*, in a few *A. boskianus* from the Iraq region and in occasional examples of some other species such as members of

the *A. pardalis* group and *A. opheodurus*. Elsewhere the subocular is shallower and the upper labials form a continuous series beneath it. The former state is likely to be plesiomorphic as it is very widespread in the Lacertidae as a whole, but the latter occurs in *Eremias* proper, in some species usually assigned to *Eremias* from the Ethiopian region and in *Meroles* Gray, 1838, *Aporosaura* Boulenger, 1887b and *Ichnotropis* Peters, 1854. The supposed apomorphic condition may apparently arise by the subocular becoming increasingly narrowed ventrally or by splitting to produce a small ventral scale that forms an extra upper labial.

In general, the subocular is separated from the lip in forms from drier, more open habitats which tend to have particularly large eyes and the character may be at least partly a functional correlate of this size increase. In species where the subocular scale usually borders the mouth, the lateral surface below the anterior eye, formed from the jugal and maxillary bones, tends to be fairly vertical, so that the scale can cover it but still remain roughly in the same plane as the upper lip of which its lower section forms part. But, with increase in eye size, the jugal arch bulges outwards and its outer face and that of the section of the maxilla below it is directed more obliquely downwards. In this situation, a single scale covering this surface and forming part of the lip would be strongly bent and possibly not able to provide the necessary flexibility for labial movement. In forms living in dry areas, the need for such movement is increased, for the upper lip projects further ventrally and is more bulky, so it and the scales covering its outer surface are displaced more during closure of the mouth, presumably producing a more efficient seal against water loss and incursion of sand particles than is present in more mesic species. Because of these changes, the replacement of the original subocular by two functional parts would probably be an advantage.

#### *Number of upper labial scales anterior to the centre of the eye.*

In the majority of forms there are typically four upper labials anterior to the centre of the eye but in some, such as the members of the *A. cantoris* group, *A. scutellatus* and *A. longipes*, five is the usual number. As four is found in forms which on other grounds seem primitive, it may be the plesiomorphic condition for *Acanthodactylus*. When present, the extra upper labial sometimes seems to develop by being split off the subocular but this may not always be its origin. In many species exceptions to the usual number occur.

#### *Parietal scales.*

*A. boueti* is singular in having the parietal scales reduced and the areas normally occupied by their lateral and posterior parts replaced by small scales.

#### *Ear opening.*

This is usually quite large but in *A. gongrorhynchatus* and *A. haasi* it is reduced in size, being occluded by skin from above and from the front. Similar reduction is found in some other lacertids that live on loose sand such as *Aporosaura* and some species of *Meroles*.

#### *Dorsal body scales.*

There is great variation in size and shape of the dorsal scales. In many species they are fine and more or less granular and either smooth or carinate, but in others size increases posteriorly and the scales become flat, more keeled and strongly imbricate. In such cases, the lateral scales tend to be smaller than the more medial ones. Transverse counts at mid-body may be as high as 100 in the most fine-scaled species, *A. longipes*, or as low as 18 in some *A. boskianus asper*. There is often substantial variation within and, more obviously, between populations of a species; thus counts vary from about 35 to 80 in *A. scutellatus* and from 18 to 52 in *A. boskianus*. This suggests that dorsal scalation is very labile so that the assessment of a primitive condition for the genus is impossible. All that can be said is that the extremes encountered in *Acanthodactylus* are near the extremes for the Lacertidae as a whole and that the primitive condition is perhaps more likely to be somewhere in between.

In some other sections of the Lacertidae, relatively fine granular scaling is usually associated with open environments while, large, keeled, strongly imbricate scales are typically found in species that live, or at least take refuge in, dense often spiny vegetation.

The latter scale arrangement provides much better mechanical protection against damage to the flexible skin between the scales, something that is potentially likely to occur when running in densely vegetated habitats. The same selective pressure may well act on *Acanthodactylus*; the most fine-scaled forms, like many populations of the *A. scutellatus* group, tend to live in the most open habitats, whereas forms like *A. boskianus* do frequently seem to take refuge in spiny vegetation (see p. 315).

*Dorsolateral tracts of enlarged scales.*

These are found on the posterior body of *A. schmidtii* and are at least indicated in some *A. blanfordii*.

*Ventral scale number.*

The number of ventral scales in the longest transverse row across the belly varies from about 8 to 18, 10 being the commonest figure. As the majority of lacertids have low numbers, these are likely to be primitive in *Acanthodactylus*. In general low numbers are most frequent in forms occupying more mesic habitats and higher ones in species living in relatively arid areas, but this correlation is imprecise. Intraspecific variation occurs, especially in forms with higher counts.

*Tessellation of ventral scales.*

Forms with high transverse counts of ventrals often have the scales tessellated, that is, they are staggered so that they do not form regular longitudinal rows. In many cases, this staggering is confined to the sides of the belly, but it may affect the median areas too. It is best and most extensively developed in most populations of the *A. scutellatus* group and in the *A. grandis* complex; it is found to a lesser extent in other members of these assemblages and is at least indicated in the *A. cantoris* group and *A. gongrorhynchatus*. There is significant variation in the extent of staggering within species where it is present. Tessellation is found in some other lacertid groups such as *Eremias* proper, *Meroles* and *Aporosaura*.

*Intergradation of dorsal and ventral scales.*

In most *Acanthodactylus*, dorsal and ventral scales are easily distinguished from each other, but in *A. gongrorhynchatus* they intergrade. This trend is also apparent in *A. haasi* and to a lesser extent in some *A. arabicus*.

*Number of rows of scales running along fingers.*

In many species there are three rows of scales running along fingers one to four, the same number that runs along each toe. One row is dorsal, one ventral and the third posterior. On finger five, and sometimes at the base of the others, there may be four rows, the additional one being anterior. In contrast, a number of forms have four regular and continuous rows of scales on all fingers; these include the *A. cantoris* and *A. scutellatus* groups, the *A. grandis* complex, *A. gongrorhynchatus* and *A. haasi*. In fact, these two conditions are not as clear cut as they appear, for a number of individuals of species that usually have three scale rows possess additional scales forming an irregular fourth row on at least some fingers; this occurs in *A. micropholis*, *A. robustus* and *A. opheodurus*. *A. masirae* habitually has four rows but these are often irregular, and *A. cantoris* in which four regular rows are usually present occasionally has the anterior one strongly reduced.

It seems likely that three scale rows running along the fingers is the primitive condition in *Acanthodactylus* for it comes closest to the two rows typical of the majority of Lacertidae and other scincomorph lizards. Three or four scale rows on the fingers also occur in *Eremias* proper, *Meroles* and *Aporosaura*. The presence of a regular fourth row is largely associated with sandy habitats. It may well allow better development of a pectination on the anterior face of the digit that matches the posterior one. This results in a wider digit that is more efficient for digging in light, unconsolidated substrates such as fine sand where *Acanthodactylus* often scrabbles for food as well as excavating burrows.



### *Pectination of the digits.*

The scales along the posterior surfaces of the digits are pointed and project to form a comb-like fringe or pectination. In some instances, this is inconspicuous but in others the scales become very long and flattened in the horizontal plane and in extreme cases, such as *A. longipes*, the fringe on the toes may be wider than the digits themselves. The scales forming the row running along the upper surfaces of the digits may project slightly forwards to produce a weak anterior fringe as well, but in species where there is an anterior scale row on the fingers, this may form a fringe approaching the posterior one in development.

There is a continuum between the weakest fringes and the most pronounced ones. Degree of development correlates very closely with what is known about the ecology of the species concerned, being least in forms living on relatively hard ground and greatest in forms from soft sand. The relationship is so strong in taxa for which some ecological information is available that it seems reasonable to use degree of pectination to predict substrate type in cases where this is unknown. The importance of fringes on the fingers for digging in loose sand has already been mentioned; fringes also enable lizards to travel across soft sand surfaces efficiently by increasing the area covered so that unit pressure is low and effort is not wasted pushing the sand backwards as the lizard moves forwards.

### *Keeling on upper caudal scales.*

Most *Acanthodactylus*, like the majority of lacertids, have keels on the dorsal scales of the tail base but these are absent in *A. (t.) tristrami*, *A. (t.) orientalis* and *A. robustus*. The restricted distribution of this feature in the Lacertidae suggests it is an apomorphy, although it has developed independently elsewhere, for instance in *Mesalina rubropunctata*.

### *Lateral processes on tail base.*

In *A. spinicauda* the lateral scales at the base of the tail are greatly enlarged, especially in males, with their keels produced to form tubercles. This feature is unique in the Lacertidae.

### *Tail length.*

In most *Acanthodactylus* the tail is more than 1.5 times the length of the head and body together but in *A. (t.) tristrami*, *A. (t.) orientalis* and *A. robustus* it is less.

### *Pattern.*

In the great majority of *Acanthodactylus* species, juveniles have a striking pattern of narrow, dark and light longitudinal stripes. The only certain exceptions are *A. schmidtii*, *A. longipes* and some *A. scutellatus* in which the newly hatched young are uniform or dappled. This condition is likely to be derived as striped patterns are very widespread among juvenile lacertids. When present, the number of dark stripes varies considerably and there may be as many as six pairs, although not all these run the whole length of the body. In the nomenclature of Lantz (1928), developed for Palearctic *Eremias*, these are 1. the *spinal* originating near the mid-line and usually fusing to produce a single stripe on the body, 2. the *occipital* arising from the hind edge of the parietal scale, 3. the *parietal* arising from the lateral edge of that scale, 4. the *temporal* beginning behind the eye and passing over the upper edge of the ear (equivalent to Lantz's upper and lower temporals), 5. the *maxillary* passing through the ear and 6. the *costal* passing below it.

It is usually acknowledged that a high number of stripes is plesiomorphic in the Lacertidae (Eimer, 1881; Boulenger, 1921; Lantz, 1928) and this condition is certainly commoner in forms which on other grounds seem primitive. Reduction in number seems to take place most usually by loss or fusion of bands at the mid-line. As we have seen, a few *Acanthodactylus* have a pair of spinal bands on the neck that fuse on the body; reduction from this state appears to follow a clear sequence: 1. the spinals fuse throughout their length; 2. the resultant composite stripe shortens while the occipital stripes fuse posterior to it; 3. the spinal stripe is reduced to a vestige or disappears and fusion of the occipitals extends forwards; 4. the occipitals fuse completely to produce a simple mid-line stripe. This means of course that mid-line stripes in *Acanthodactylus* are not always homologous as they can be



composed either of fused spinal bands or of occipitals. There may also be loss of the outermost bands, especially the costals on the body.

Presence of a pair of spinal stripes on the neck is largely confined to some *A. micropholis*, *A. erythrurus* and *A. pardalis*. The partial development of a mid-dorsal stripe made up of the occipitals occurs in some individuals of the following species: *A. boskianus*, *A. schreiberi*, *A. pardalis*, *A. scutellatus*, *A. opheodurus*, *A. felcis* and *A. masirae*, but complete fusion seems to be confined to some *A. boskianus* and *A. scutellatus* and most *A. opheodurus*.

*A. micropholis* retains a simple striped pattern throughout life. In other forms this is often modified, but predominantly striped individuals, or ones with longitudinal rows of spots, are common in most species. However not all the stripes present in juveniles may be discernible in these adults.

*A. pardalis* and *A. maculatus* are singular in that some individuals of each have spots of brownish red pigment on their backs that do not fade or disappear in alcohol.

In *A. (t.) tristrami*, *A. (t.) orientalis* and *A. robustus* some individuals have two rows of large ocellar markings along the back.

### Species boundaries and species groups

The introduction of osteological and especially hemipenial characters provides a partial test of the homogeneity of the species presently recognized within *Acanthodactylus*. For even if the external features on which these nominal taxa are based show little obvious variation, discontinuity in characters from the new sources may indicate that more than one form is involved. The species are mostly discussed below in groups that consist of species with a high level of overall similarity and which, in most cases, probably form holophyletic assemblages, although there are exceptions.

#### *A. micropholis*

*A. micropholis* Blanford, 1874a, occurs in southeast Iran and southwest Pakistan, in the latter country occupying sandy places along water courses in hilly areas (Minton, 1966). It has a high proportion of primitive features including the following: premaxilla with about seven teeth and not abruptly narrowed, 24 presacral vertebrae in males and 25 in females, sternal ribs usually intact; hemipenis and armature fairly symmetrical, clavulae flattened and simple, connectors slender; subocular often reaching mouth, frequently four upper labials anterior to centre of eye, eight or ten ventrals in longest row across belly, ventrals arranged in straight longitudinal rows, usually three longitudinal rows of scales on fingers, pectination on digits rather weak, upper caudal scales keeled, young with numerous dorsal stripes which are retained by adults. On the other hand, the first and fourth supraoculars are broken up and, in some individuals, the subocular may be separated from the mouth, five upper labials are sometimes present anterior to the centre of the eye and there may be indications of a fourth scale row on the fingers.

#### The *A. cantoris* group, *A. gongrorhynchatus* and *A. haasi*

*A. cantoris* Günther, 1864b: NW. India, Pakistan, E. Afghanistan.

*A. blanfordii* Boulenger, 1918a: S. Afghanistan, SW. Pakistan, SE, Iran, Oman (Muscat area).

*A. schmidtii* Haas, 1957: Arabia except extreme west; SW. Iran (Anderson, 1963, 1974).

*A. arabicus* Boulenger, 1918a: SW. Arabia.

*A. gongrorhynchatus* Leviton & Anderson, 1967: E. and SE. Arabia.

*A. haasi* Leviton & Anderson, 1967: E. Arabia (Dhahran).

The first four forms, which constitute the *A. cantoris* group, are all associated with loose sand habitats (*A. cantoris*—Minton, 1966; Mertens, 1969, *A. blanfordii*—Blanford, 1874b; Anderson, 1963; Clark *et al.*, 1969; M. D. Gallagher, pers. comm. *A. schmidtii*—Anderson, 1963; personal observations, *A. arabicus*—Anderson, 1895). Soft ground types are also

suggested by the extensive pectination of the digits. Members of the *A. cantoris* group share the following features: premaxilla with about seven teeth and usually abruptly narrowed (least in *A. cantoris*), usually 24 presacral vertebrae in males, 25 in females (less sexual differentiation in some populations of *A. schmidtii*), fifth sternal rib often intact; hemipenis and armature usually showing marked asymmetry (not in most *A. cantoris*), clavulae not very complex, connectors relatively slender; first supraocular intact or not much divided and the fourth large or rather fragmented with a group of granules wedged between it and the third, subocular nearly always separated from the mouth, usually five upper labials anterior to the centre of the eye, posterior dorsals coarse and carinate, 12–18 ventrals in longest row across belly, ventrals arranged in fairly straight longitudinal rows, although sometimes staggered at sides, nearly always four longitudinal rows of scales on fingers (anterior row sometimes reduced in *A. cantoris*), pectination on digits strong, upper caudal scales keeled, young usually with numerous dorsal stripes (not in *A. schmidtii*) that are typically lost in adults.

In the past it has been usual to treat these four forms as subspecies of *A. cantoris*. But,

**Table 2** Variation in the *A. cantoris* group

	<i>A. cantoris</i>	<i>A. blanfordii</i>	<i>A. schmidtii</i>	<i>A. arabicus</i>
Hemipenis size	small	large	large	large
medial lobe	unreduced	somewhat reduced	minute or absent	minute or absent
medial side of armature	virtually unreduced	somewhat reduced	usually absent	absent
lateral clavula	flat and simple	lobed and pocketed	lobed and sometimes pocketed	very narrow
Postorbital and postfrontal bones	fused	separate	separate	separate
Sexual variation in number of presacral vertebrae	yes	yes	not in populations from United Arab Emirates	yes
Dorsal scales across mid-body	26–36	30–46	33–51	27–35
Dorsolateral tracts of enlarged scales on hind back	no	indicated in some cases	yes	no
Number of ventral scales in longest row across belly	12(14)	(11)12–14(16)	13–18	(12)14–16
Juveniles with dorsal stripes	yes	yes	no	yes
Adults striped or with rows of dark spots	sometimes	sometimes (all animals from Muscat)	no	in west of range
Tail with transverse bands	no	no	in juveniles and many adults	no
Maximum size within populations (snout-vent, mm)	77	60–75	67–105	55–63

although they have a strong overall resemblance to each other and, so far as is known, are allopatric, each has a number of distinctive characters that are often more pronounced than those separating accepted species of *Acanthodactylus* (see Table 2). Because of this, it seems more consistent to give them full species status.

*A. cantoris* is widespread in northwest India and in Pakistan is found in the southeast and in the Indus drainage whence it reaches east Afghanistan (Kabul River area, CAS 96200-01, 120358-60); it also extends westwards along the Pakistan coast at least to Ormara (BM(NH) 1904.12.7.2; Minton, 1966, records *A. blanfordii* from this locality but his specimens, RSM 1964.58.2/6, are in fact *A. cantoris*). There is some geographical variation, for instance in the Punjab the anterior row of scales on the fingers is incomplete in some animals. This is true of a female from Cambellpur (BM(NH) 1933.5.16.8) which is also peculiar in having a rather blunt snout and elongate, strongly overlapping dorsal scales.

*A. blanfordii* reaches its easternmost limit in the Helmand drainage of south Afghanistan and the neighbouring border area of Pakistan (BM(NH) 86.9.21.77-80; Mertens, 1969; it is also probable that the specimens listed by Clark *et al.*, 1969, and Minton, 1966 are *A. blanfordii*). *A. blanfordii* and *A. cantoris* may be separated by intervening high ground in this area but it is possible that they meet on the coast for *A. blanfordii* extends eastwards as far as Pasni (Mertens, 1969), only about 130 km from the nearest known *A. cantoris* locality. The differences in dorsal and gular scale counts on which these two forms were originally separated do not always hold but they can be distinguished by the fusion of postorbital and postfrontal bones in *A. cantoris* and by hemipenial features. *A. blanfordii* extends into eastern Iran at least as far as the Bandar Abbas region (Anderson, 1963) and an isolated population has recently been found by M. D. Gallagher near Muscat, southeast Arabia (BM(NH) 1973.723-26, 1976. 1462-64, 1977.68-69); here all the adults examined retain at least traces of dorsal striping.

*A. schmidtii* is widespread in Arabia where it shows substantial regional variation in body size (Arnold, 1981*b*). It also extends into southwest Iran (Anderson, 1974) but without apparently contacting *A. blanfordii*.

*A. arabicus* is restricted to the littoral area of southwest Arabia and seems to be separated from *A. schmidtii* by hilly, not very sandy country occupied by such species as *A. boskianus*, *A. felcis* and *A. ophiodurus*. Although *A. arabicus* and *A. schmidtii* both have the medial side of the hemipenis and armature very reduced, they differ in their other apparent apomorphies (*A. arabicus*—very narrow clavula; *A. schmidtii*—often very large size, dorsolateral tracts of enlarged scales on hind back, lack of stripes in juvenile and adult patterns) and in dorsal scale number. In fact *A. arabicus* is more similar to *A. blanfordii*, especially Muscat specimens, differing mainly in its more slender build, greater hemipenial asymmetry, narrower clavula and higher number of ventral scales across the belly (usually 14-16 as against 11-13(14) at Muscat). *A. arabicus* from Aden and its vicinity are comparatively large and usually retain stripes or spots when adult but animals from further east (as far as Gischin (= Qishn), NMW 11814/1-16) are smaller and often become uniform in colouring with maturity.

Relationships within the *A. cantoris* group are not easy to discern with great certainty, since most of the apomorphies available for judging affinities are rather weak (see p. 324), but *A. blanfordii*, *A. schmidtii* and *A. arabicus* all differ from *A. cantoris* in their more narrowed premaxillae, more asymmetrical hemipenes and usually higher number of ventrals, while lacking its fused postorbital and postfrontal bones and its hemipenial peculiarities (p. 305), so they may well form a distinct unit with *A. blanfordii* as the least modified species. Within it, *A. schmidtii* and *A. arabicus* share almost total loss of the medial side of the hemipenis and armature, but there are no other apparent synapomorphies joining them, apart from increase in ventral scale count. As extreme hemipenial asymmetry has developed a number of times within *Acanthodactylus*, its value as an indicator of relationship is quite low. It is possible that *A. schmidtii* is the sister species of *A. blanfordii* for the latter occasionally shows indications of the dorsolateral tracts of enlarged scales on the hind-back that are typical of



the former and they often share a peculiar lateral clavula shape in which there is a proximally directed pocket. Moreover, *A. schmidtii* occasionally has a medial clavula exactly like that of *A. blanfordii*. Certainly *A. arabicus* and *A. schmidtii* are more like *A. blanfordii* than like each other and may well have been independently derived from a *A. blanfordii*-like stock.

*A. gongrorhynchatus* is sympatric with *A. schmidtii* in east and southeast Arabia and shares many features of the *A. cantoris* group but it differs in its very slender adult build, convex pileus, short but abruptly acuminate snout, weakly keeled supratemporal scales that are fragmented posteriorly, four upper labials anterior to the centre of the eye, an ear hole that is reduced in size and fine dorsal scaling that sometimes grades into the ventral scales. Recent observations by Mr W. Ross (personal communication) show that *A. gongrorhynchatus* lives on aeolian sand. Its morphology—depressed fingers, strong digital pectination, very pointed snout and partly occluded ear opening—is appropriate for such a substrate and suggests that it is more strictly confined to this habitat than *A. schmidtii* which occupies the same general area. *A. gongrorhynchatus* may well be paedomorphic in some features which are typical of juvenile *Acanthodactylus*, for instance the rounded pileus, short snout and lack of strong keeling on the supratemporal scales. In fact it has substantial resemblance to immature specimens of *A. arabicus* and may well be closely related to this species, especially as their hemipenes are very similar including the very narrow lateral clavula.

The present situation in Arabia may have arisen by a second stock of the *A. cantoris* group invading to exist alongside one already present. It is possible that much of the peninsula was originally occupied by *A. arabicus*-like populations and that the precursor of *A. schmidtii* entered the area from the east to become sympatric with them, except in the extreme south-west littoral region which is isolated by geographical barriers. Here *A. arabicus* survives but elsewhere coexistence of two species in soft-sand habitats favoured by the *A. cantoris* group would be expected to produce considerable character displacement, the *A. arabicus*-like stock giving rise to *A. gongrorhynchatus* and the invading one to *A. schmidtii*, the two most divergent species in the assemblage. An analogous situation exists among the nocturnal ground geckoes of the genus *Stenodactylus* that occupy soft sand habitats (Arnold, 1980a). As in *Acanthodactylus* there is a single species in the southwestern littoral region of Arabia (*S. pulcher*) which has a close relative widespread in the peninsula (*S. arabicus*), where it is sympatric with another more distantly related species (*S. doriae*). As with *A. gongrorhynchatus*, *S. arabicus* is more strongly adapted to sandy environments and smaller than its southwestern relative whereas *S. doriae*, like *A. schmidtii* is relatively large.

*A. haasi* is known only from the male holotype obtained at Dahrán, eastern Saudi Arabia. In spite of being collected in 1946, no further examples have appeared, even though a great deal of *Acanthodactylus* material has been taken in the general area. *A. haasi* has much in common with *A. gongrorhynchatus* and shares a number of synapomorphies with it that occur nowhere else in the genus; these include very slender habitus, similar lateral clavula structure and reduced ear opening. It differs in its less acuminate snout and less narrowed premaxilla, shorter lateral clavula, five upper labials anterior to the centre of the eye, large and weakly keeled dorsal scales, less pectination on the fingers and numerous keels on the subdigital lamellae. In most of these features and many others *A. haasi* resembles members of the *A. cantoris* group from which *A. gongrorhynchatus* is probably derived. This together with the synapomorphies shared with the latter may indicate that *A. haasi* and *A. gongrorhynchatus* are sister species.

Another possibility, suggested partly by the fact that no further specimens have been collected, is that *A. haasi* is a hybrid between *A. gongrorhynchatus* and one of the other *Acanthodactylus* species in eastern Arabia. Assuming that a hybrid would probably be intermediate in many features, the various candidates can be considered in turn. *A. schmidtii* is unlikely because its premaxilla is constricted, it has a high number of ventral scales in the longest row across the belly (13–18 compared with 10–12 in *A. gongrorhynchatus* and 12 in *A. haasi*), pectination on the fingers is extensive, multiple carination on the digits is absent



(present in *A. haasi*) and, in east Arabia, it is a far larger animal than *A. gongrorhynchatus*, so interspecific copulation is unlikely; size difference would probably also exclude *A. boskianus* as well. *A. scutellatus* has a narrow premaxilla with only five teeth, dorsal scaling is fine and again there is no multiple carination on the digits. *A. opheodurus* has this feature in at least some cases and possesses all the other characteristics to be expected if *A. haasi* is a hybrid between it and *A. gongrorhynchatus*. But the status of *A. haasi* will probably only be decided by further collection in the area of the type locality.

### *A. schreiberi* and *A. boskianus*

*A. schreiberi* Boulenger, 1878; Cyprus, Lebanon, N. Israel.

*A. boskianus* (Daudin, 1802): Much of north Africa as far south as N. Nigeria and Eritrea, Arabia but not the R'ub al Khali, S. Israel, Jordan, Iraq, Syria and adjoining Turkey.

These species are rarely found on very soft sand surfaces but occur on more stable sand and other harder substrates. *A. boskianus* is often associated with quite dense, sometimes spiny vegetation, although it also forages in more open areas (Doumergue, 1901; Flower, 1933; field labels attached to BM specimens; personal observations in southeast Arabia). Both species share a relatively high number of primitive features including the following: premaxilla with about seven teeth and not abruptly narrowed, usually 24 presacral vertebrae in males and 25 in females; fifth sternal rib often intact, hemipenis more or less symmetrical, medial side of clavula not strongly reduced; supraoculars more or less intact (first sometimes divided in *A. boskianus*), usually four upper labials anterior to centre of eye, typically 10 ventral scales in longest row across belly (12 in many Arabian *A. boskianus*), ventrals arranged in straight longitudinal rows, three longitudinal rows of scales on fingers, pectination on digits not exceptionally strong, upper caudal scales keeled, young with numerous dorsal stripes that are sometimes retained in modified form by adults. Apparently apomorphic characters include reduction of the proximal lip of the medial branch of the hemipenial sulcus, some reduction of medial side of armature, medial clavula pointed with a  $\pi$ -shaped cross section, lateral clavula complexly lobed, most medial of the lateral connectors broad; subocular does not usually reach mouth (exceptions in *A. boskianus*) and dorsal scales are often large. The close resemblance of *A. schreiberi* and *A. boskianus* together with the close match of their hemipenes in apomorphic features makes it very probable that they are sister species.

*A. schreiberi* has two allopatric populations: *A. s. schreiberi* on Cyprus and *A. schreiberi syriacus* Boettger, 1879 in Lebanon and north Israel, the latter having coarser dorsal scales with sharper keels. *A. boskianus* usually differs most obviously from *A. schreiberi* in possessing larger dorsal scales. However there is slight overlap in the transverse scale counts between the hind limbs, but not in Israel where the two species appear to contact each other without introgression (Duvdevani and Borut, 1974b). *A. boskianus* is the most widely distributed species of its genus but the range is not continuous in northern Africa where this lizard is mainly restricted to the periphery of the Saharan desert and to oases and other fairly mesic areas within it. As the species is relatively uniform in this region, its spread to these isolated areas may have been quite recent, presumably during one of the episodes in the Quaternary when conditions in north Africa were less extreme.

*A. boskianus* has been divided into three subspecies: *A. b. boskianus* in the Nile delta area and parts of Sinai; *A. b. euphraticus* Boulenger, 1919 described from Ramadieh (= Ramdi, Iraq) and *A. b. asper* (Audouin, 1829) which covers almost the whole of the species' range. This simple, tripartite division is not satisfactory, for some of the supposedly distinctive features of *A. b. euphraticus* are not consistent and there is some differentiation within the populations assigned to *A. b. asper*. An adequate intraspecific treatment of *A. boskianus* is beyond the scope of this paper but variation of some features within the species will be

briefly described. Over most of north Africa, the number of dorsal scales in a transverse row at mid-body varies from about 26 to 41, although maxima are less in many areas, the first supraocular scale is usually intact and the subocular does not reach the mouth in most individuals. In the Nile delta and north Sinai, populations assigned to *A. b. boskianus* have high dorsal scale counts (34–52) and the supraocular scale is divided, but these populations intergrade with those typical of the rest of north Africa and with similar ones in Israel and west Jordan. Animals with high dorsal counts (38–48) also occur in northeast Jordan, north and central Iraq, east Syria and adjoining Turkey. In some cases, such as the types of *A. b. euphraticus*, they also have the first supraocular divided and the subocular often meeting the mouth, but these conditions are absent in many individuals from neighbouring populations. Arabian animals are rather similar to those widespread in north Africa but are characterized by low transverse dorsal scale counts at mid-body (usually 18–27 but up to 36 in the south-western mountains) and a large body size (up to 93 mm from snout to vent against maxima of about 82 elsewhere; specimens from the western periphery of the peninsula tend to be smaller). Arabian *A. boskianus* contrast strongly with those found to the north. In Jordan an animal from the southeast of the country (El Inab, JUM R505) is of the Arabian type whereas those from elsewhere are less coarsely scaled (31–37 scales across mid-back) and relatively small (only up to about 65 mm from snout to vent). Animals of this type occur at Wadi Rum (JUM R69), only about 130 km from El Inab. Whether the two forms intergrade and, if so, whether the intergradation is abrupt is not known.

Geographical variation in *A. boskianus* may well reflect differences in niche across its range. As stated, this species is often associated with dense vegetation and large dorsal scales may well be protective where shrubs are rigid and spiny; the fine-scaled populations are in relatively mesic areas (Nile Delta, Tigris–Euphrates river system) where vegetation would be expected to be less damaging than in more arid regions. Division of the first supraocular scale and a subocular that reaches the mouth are also characters typical of more mesic situations (see p. 307). The distinctive features of lowland Arabian *A. boskianus* may be related to the fact that they coexist here with *A. opheodurus*, a small form originally confused with *A. boskianus* that occupies similar substrates and occurs in strict sympatry with it, at least in some areas (Arnold, 1980b). The presence of *A. opheodurus* might have produced displacement or restriction of the niche available to *A. boskianus* with consequent morphological change (Arnold, 1981b). Thus, increase in body size may allow adult *A. boskianus* to take larger prey, reducing competition for small food items; very large scale size could indicate that this species spends a higher proportion of time in vegetation than elsewhere. It is perhaps significant that in extreme southwest Arabia, where no *A. opheodurus* are known, *A. boskianus* is smaller with higher dorsal scale counts than elsewhere in the peninsula.

In spite of the considerable variation encountered in *A. boskianus*, as presently understood, there is as yet no firm evidence that it consists of more than one species. However, *A. schreiberi* may well have originated as an isolate of *A. boskianus*.

### The *A. grandis* complex

*A. grandis* Boulenger, 1909 complex (including *A. fraseri* Boulenger, 1918c): Syria, E. Lebanon, Jordan, NW. Arabia, Iraq, SW. Iran (Khuzistan and Fars provinces—Anderson, 1974).

Nothing certain is known about the ecology of these lizards but the restricted pectination on the digits suggests that they are not usually found on very soft sand surfaces; however there is some variation in this feature between populations which may indicate that they occupy a variety of ground types. The members of the *A. grandis* complex share many features with *A. schreiberi* and *A. boskianus*, especially the former, the most significant differences being that, in the *A. grandis* complex, the ventrals are tessellated and the number in the longest row across the belly is higher (14–18), there are four longitudinal series of scales running along the fingers and the hemipenis, although generally very similar often differs slightly in the pattern of lobing on the upper surface of the lateral clavula (p. 306); also, five upper labial scales are more frequently present anterior to the centre of the eye.

**Table 3** *A. grandis* complex: variation between samples

Locality	n	Maximum snout-vent length of available adults	Dorsal scales in transverse row at mid-body	Strength of keeling on dorsal scales (0=none, 4=strong)	Ventral scales in longest row across belly	Projections on free edges of sub-digital lamellae
JORDAN and SYRIA (BM, MCZ56647, including types of <i>A. grandis</i> )	6	♂103	56–64	0	16–18	several
IRAQ (localities listed from northwest to southeast)						
Hatrah, Ninevah Prov. (INHM)	2	♂70	47, 49	2	14	several
Rawa Desert (BM)	2	—	49	1	14	several
Jabal Hamrin (INHM)	1	♀62	49	4	17	several
Between Baghdad and Falluja (BM)	4	—	43–50	3	17	several
Al Uzaym, Dijla Prov. (INHM)	1	♂90	53	1	15	one
Shthath, Kerbala (INHM)	1	—	51	1	14	one
25 km S. of Najaf (INHM)	1	♂76	50	2	16	one
Nassiryah (BM)	1	♂78	49	4	16	one
Zubeya (= Az Zubayr, BM, types of <i>A.</i> <i>fraseri</i> )		♂73	48, 50	4	16	one
SW.IRAN (USNM 13500–01)	2	♂63	42, 44	4	14–16	one

*A. grandis* was originally described from the Damascus area of Syria while the only other nominal species assignable to the complex, *A. fraseri*, is based on material from Zobeya, Shariba (=Shu'aiba, northeast of Basra) far to the east in southeastern Iraq. Material collected subsequently in the intervening areas shows a variety of conditions intermediate between the named forms but the pattern of variation appears to be irregular and sometimes animals from adjacent localities show considerable differences in such features as adult size, strength of keeling on the dorsal scales, and pattern (summarized in Table 3). In general, members of the eastern populations tend to be smaller than western animals with fewer, more strongly keeled dorsal scales and single points on each subdigital lamella.

It is possible that the *A. grandis* complex is best regarded as a single species but available samples are too small and scattered to be certain about this. The irregular variation of populations intermediate between typical *A. grandis* and *A. fraseri* may reflect the geography of Mesopotamia, for here the comparatively arid country favoured by *Acanthodactylus* is divided up by the Tigris and Euphrates rivers and their tributaries which flood seasonally, so populations may be substantially discontinuous. Other *Acanthodactylus* species, especially *A. boskianus*, also show considerable variation in this area.



### The *A. tristrami* group

*A. (t.) tristrami* (Günther, 1864): Lebanon, SW. Syria, NW. Jordan.

*A. (t.) orientalis* Angel, 1936: E. Syria, W. and central Iraq.

*A. robustus* Werner, 1929: S. Syria, SW. Iraq, Jordan and N. Arabia.

The weak digital pectination in these forms suggests that they are found on fairly hard substrates. *A. (t.) tristrami* seems to be confined to steppe-type habitats on the edge of the Anti-Lebanon range. *A. (t.) orientalis* may also be restricted to relatively mesic habitats since most records are from localities on or near the Tigris–Euphrates river system (Angel, 1936; Schmidt, 1939; Haas and Werner, 1969), although Angel also records it from Palmyra. *A. robustus*, on the other hand seems to occupy more desertic regions; Riney (1953) gives brief ecological notes that refer to this species, although they are attributed to *A. (t.) orientalis*.

Typical *A. tristrami* has many features in common with *A. schreiberi* (p. 315) but there are a number of differences: there are more presacral vertebrae, with about 25 in males and 26 or 27 in females, the proximal lip of the medial branch of the hemipenial sulcus is not reduced, the lateral clavula is complex but not lobed and is very slightly bifurcate at its tip, the first and fourth supraoculars are fragmented, the subocular reaches the mouth, the dorsal and upper caudal scales lack keels and the tail is short. Of these features, fragmentation of the supraoculars, unkeeled upper caudals, short tail, clavula shape, and perhaps vertebral number may be regarded as apomorphies. Nearly all occur in other populations of the *A. tristrami* group and unkeeled upper caudals and the short tail are confined to it.

Two other subspecies assigned to *A. tristrami* have been named, *A. t. orientalis* from eastern Syria and *A. t. iracensis*, Schmidt, 1939, described from Haditha on the Euphrates in west Iraq. The latter is said to have a lower mid-body dorsal scale count (45–46 against 48–56) and a weaker dorsal pattern than *A. t. orientalis* but other material from the same area (Haas & Werner, 1969) and from Najaf, further down the Euphrates (INHM, with 51 dorsal scales at mid-body and a bold pattern) suggest that this distinction is illusory. *A. t. iracensis* is therefore referred to the synonymy of *orientalis*. As understood here, this form is distinguished from typical *tristrami* by its smaller size (up to 63 mm from snout to vent instead of up to 92 mm) and fewer dorsal scales (43–56 against 54–65). The hemipenes are also distinctive, *orientalis* having the medial lobe and medial side of the armature very reduced. These differences suggest that *tristrami* and *orientalis* might be better regarded as full species but more information is needed before this can be confirmed.

*A. robustus* shares most of the distinctive features of *A. (t.) tristrami* but the lateral clavula is relatively simple, the snout is shorter and more pointed, the subocular frequently separated from the mouth, there are often 12 instead of 10 ventrals in the longest row across the belly and there may be a rudimentary fourth longitudinal row of scales on the fingers.

### *A. erythrurus* group

*A. erythrurus* (Schinz, 1833): Spain, Portugal, Morocco, N. Algeria.

*A. savignyi* (Audouin, 1829): N. Algeria, N. Tunisia.

*A. boueti* Chabanaud, 1917: N. Dahomey, N. Ghana.

*A. guineensis* (Boulenger, 1887a): Ghana, Nigeria, Niger and Cameroon.

These species are typical of relatively mesic areas and usually have weak digital pectination. They are similar to *A. (t.) tristrami* in many features but all lack the short tail and unkeeled upper caudal scales of this form and also frequently have an azygos shield between the prefrontal scales.

In *A. erythrurus* and *A. savignyi* the lateral clavula of the hemipenis is deeply bifurcate at its tip, the frontonasal scale is quite often divided and the subocular may be separated from the lip.

*A. erythrurus* has three widespread forms: *A. e. erythrurus* in Spain and Portugal *A. e. lineomaculatus* Duméril & Bibron, 1839 in lowland western Morocco and *A. e. bellii* Gray,



1845 in the adjoining higher country and in north Algeria. Each of these is well defined on external features and *A. e. bellii* is further distinguished by its usually simple lateral clavula. Two other subspecies are sometimes recognized: *A. e. mauritanicus*, Doumergue, 1901 of extreme northern Algeria resembles *A. e. bellii* in most features including its lateral clavula and differs only in its more obviously keeled dorsals; *A. e. atlanticus* Boulenger, 1918a has a restricted distribution in north Morocco between the ranges of *A. e. bellii* and *A. e. lineomaculatus* and may be an intermediate between them. *A. savignyi blanci* Doumergue, 1901 of north Tunisia is very similar to *A. e. lineomaculatus* but *A. s. savignyi* which coexists with *A. erythrurus* in north Algeria is more distinctive. It has a clearly pointed snout and a better developed pectination on the digits than is usual in its close relatives which may be related to its occupying more sandy habitats (Doumergue, 1901). It is possible that the differences between the two subspecies of *A. savignyi* are a result of character displacement (Arnold, 1981b).

*A. boueti* and *A. guineensis* are generally like the above but the frontonasal is undivided and the subocular scale is never separated from the lip. Each species has a number of distinctive features. In *A. boueti* there are nine premaxillary teeth, the hemipenis is very small, the second supraocular scale is broken up and the parietal scales are partly fragmented. *A. guineensis* has the medial side of the hemipenis and armature absent and a peculiar arrangement of nasal scales (p. 296), a feature that occurs rarely also in *A. erythrurus*.

### The *A. pardalis* group

*A. p. pardalis* (Lichtenstein, 1823): Cyrenaica, north Egypt, Israel.

*A. p. bedriagai* Lataste, 1881: High plateaux of north Algeria (provinces of Oran, Algiers and Constantine); closely related populations in west Morocco and west Tunisia.

*A. maculatus* (Gray, 1838): northeast Morocco, north Algeria, Tunisia, Tripolitania.

*A. spinicauda* Doumergue, 1901: Arba Tahtani and El Abiodh Sidi Sheikh, northwest Algeria.

Members of the *A. pardalis* group are largely confined to relatively hard compact substrates such as clayey-sandy soils, clay, loess and salt flats (Blanc, 1980; Gauthier, 1967; Mosauer, 1934; data on labels attached to BM(NH) specimens).

They all agree in the following characters: premaxilla with about seven teeth, not narrowed and separated from the maxillae by a constriction. presacral vertebrae usually 24–26 in males and 25–26 in females, fifth sternal rib often interrupted; hemipenis and armature asymmetrical, often markedly so, lateral clavula often bifurcate at tip, lateral connectors often thickened; first supraocular intact or not very much divided and the fourth fragmented, subocular separated from mouth, four or five upper labials anterior to centre of eye, dorsals small and often more or less smooth, 12 or more ventrals in longest row across belly, ventrals arranged in fairly straight longitudinal rows, three longitudinal rows of scales on fingers, pectination on digits relatively weak although somewhat variable, young with numerous dorsal stripes.

Boulenger (1918a, 1921) treated the *A. pardalis* group as a single species within which he recognized five varieties: *pardalis* (his forma typica), *bedriagai*, *maculatus*, *latastii* Boulenger, 1918a and *spinicauda*. Pasteur & Bons (1960) regarded *spinicauda* as a distinct species but felt that the other varieties were no more than individual variations and placed them in the synonymy of the monotypic species *A. pardalis*. In fact, the introduction of osteological and hemipenial data helps to confirm the validity of the majority of Boulenger's divisions and it appears that at least five entities within the *A. pardalis* group can be recognized (see Table 4 & Fig. 7), *A. maculatus*, as understood here, includes Boulenger's var. *latastii*. This author restricted *maculatus* to often relatively small-bodied populations in which the posterior dorsal scales are frequently keeled and some individuals have light stripes or rows of light spots. These are distributed along the coastal areas of Tripolitania and

Table 4 Variation within the *Acanthodactylus pardalis* group

	<i>A. p.</i> <i>pardalis</i>	<i>A. p.</i> <i>bedriagai</i>	Un-named west Moroccan population	<i>A.</i> <i>maculatus</i>	<i>A.</i> <i>spinicauda</i>
Hemipenis lacks medial lobe and medial section of armature	—	—*	—	+	+
Usual number of presacral vertebrae: males	24/25	26	26	24	24
females	25(26)	26	26	25	26
Approximate number of animals in which 5th sternal rib is interrupted	20/24	7/14	4/9	48/62	7/10
Number of ventral scales in longest transverse row	12(14)	14(12, 16)	12	12(14)	12
Longitudinal rows of ventral scales	27–34	31–36	30–34	27–33	27–33
Keeling on dorsal scales often quite strong	—	—	+	+ / —	+
Enlarged, tubercular scales on sides of tail base	—	—	—	—	+

\*excluding population from Tamesmida, see below.

Tunisia and in northeast Algeria. The name *latastii* was applied to inland populations lying mainly to the south in which body size is sometimes greater, dorsal scales are usually more or less smooth, the dorsal pattern tends to lack light stripes or spots and the snout is more pointed. However, there is considerable variation and many intermediates occur, so it seems best to regard these populations as a single unit. The geographical differences within this may reflect change in vegetation and substrate conditions; the pattern of *maculatus*-type animals is more likely to be cryptic where vegetation is relatively dense whilst that typical of *latastii* is probably cryptic in more open areas.

The relationships between the forms described in Table 4 are not entirely clear, but it is certain that they cannot all be assigned to a single species. Although no areas of certain sympatry are known, *bedriagai*, the form of the high plateaux of north Algeria, approaches the more southern *maculatus* near Biskra (*bedriagai*—Aures Mountains north of Biskra, BM(NH) 91.5.4.70–72; *maculatus*—near Biskra, BM(NH) 1907.4.6.10–25, BM(NH) 1920.1.20.791, BM(NH) 1969.2121–23). The two localities are probably within 100 km of each other but the forms retain their differences in hemipenial structure, usual number of presacral vertebrae and of ventral scales in the longest row across the belly, and in pattern. It seems likely therefore that *bedriagai* and *maculatus* are distinct species, especially as the hemipenial differences between them could act as an isolating mechanism.

The un-named west Moroccan population (north of Agadir, BM(NH) 1970.246–47; 20 km north of Tiznit, BM 1970.248; 30 km southwest of Goulmime, BM(NH) 1970.249–50) is generally similar to *bedriagai* and is probably conspecific with it but differs in the following features: snout often more pointed, posterior dorsal scales more pointed and keeled, ventrals in longest row across belly often 12 (not 14), upper labials anterior to centre of eye often four (frequently five in *bedriagai*), range of dorsal patterns somewhat different. It is possible that this population also contacts *A. maculatus* although evidence is lacking.

Another *A. bedriagai*-like population occurs at Tamesmida (33.05N 8.23E) in western Tunisia (BM(NH) 1920.1.20.3018, discussed by Boulenger, 1921, p. 67). The two male specimens available resemble this form very closely in osteological features and externals but the hemipenis is single-lobed and the median side of the armature is lacking. Close by at

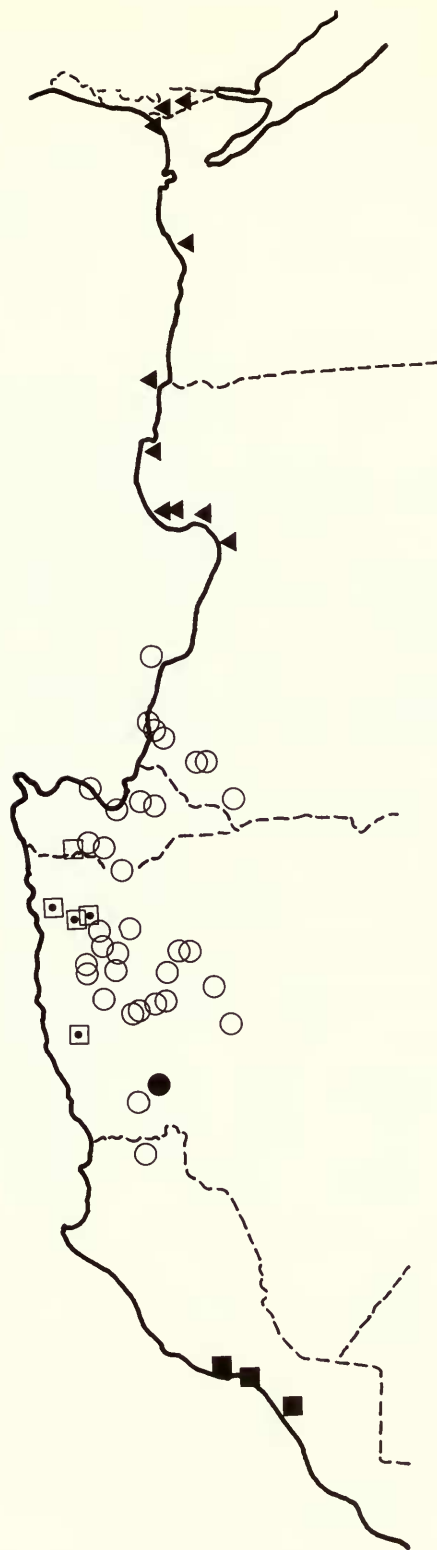


Fig. 7 Distribution of the *A. pardalis* group based largely on material in the British Museum (Natural History). ▲—*A. p. pardalis*; □—*A. p. bedriagai*; □—*A. p. bedriagai*-like population from near Tamesmida (see p. 000); ■—unnamed West Moroccan population similar to *A. p. bedriagai*; ○—*A. maculatus*, ●—*A. spinicauda*.

Furryanah (34.57N 8.35E), *A. maculatus* occurs (BM(NH) 1920.1.20.3018e) but, as the Tamesmida specimens are not like this form in other respects, a hybrid origin for them seems unlikely. Possibly they represent an isolate of the *A. bedriagai* stock that has undergone hemipenial modification in response to some previous threat of introgression, as seems to have happened several times in *Acanthodactylus* (p. 304). Tamesmida is on the edge of the eastern extension of the high ground on which *A. bedriagai* is found.

The form *spinicauda* is known only from Arba Tahtani (= Arbaouat, 33.05N 00.35E) and nearby El Abior Sidi Sheikh (= El Abiodh Sidi Cheikh, 32.53N 00.34E), oases at the southern foot of the Saharan Atlas in northwest Algeria. In general form, hemipenial structure and pattern, it resembles *A. maculatus* populations in the region (Mecheria and Laghouat) but differs in having the lateral scales at the base of the tail greatly enlarged, especially in males, with their keels produced to form tubercles, this condition occurring in no other lacertid. The hind legs are also rather longer than in nearby *A. maculatus* populations, although this is partly due to the fact that relative hind-leg length decreases with size and *spinicauda* is quite small; three females radiographed all have 26 presacral vertebrae instead of the 25 usual in *A. maculatus*. The two forms do not appear to be sympatric, so a direct test of the species status of *spinicauda* is not possible. It is certainly very like neighbouring *A. maculatus* but the three distinctive features, especially the unique tail structure, suggest it may be best to regard it as a full species, at least for the present. In the south of its range, *maculatus* appears to have a disjunct distribution, occurring mainly around oases such as Ouargla, Ghardia and Leghouat. Presumably its range was once more continuous but has become fragmented since the climate of the area has become more extreme. It is probable that *A. spinicauda* originated from such an oasis isolate.

Typical *A. pardalis* show some variation, for instance animals from the Jebel el Akhdar region of Cyrenaica appear to be smaller than samples to the south and east. Also, although Egyptian animals usually have 24 presacral vertebrae in males and 25 in females, in Cyrenaica 25 is common in males and females sometimes have 26. While there is evidence that *bedriagai* and *maculatus* are specifically distinct, it is less clear how they are related to typical *A. pardalis*. This is partly because neither is known to contact this form, there being a gap in the known range of the *A. pardalis* group as a whole south of the Gulf of Sirte, Libya, although whether this is real or a collecting artifact is uncertain. Typical *A. pardalis* resembles *bedriagai* in hemipenial structure but differs in usual number of presacral vertebrae and ventral scales in the longest row across the belly (although the *bedriagai*-like population in west Morocco matches *pardalis* in this last characteristic). On the other hand, *A. pardalis* resembles *maculatus* in these features and the nearest populations of each form are quite similar, although coastal *maculatus* west of the Gulf of Sirte are smaller and have more strongly keeled dorsal scales than the closest *pardalis*. However, these two forms differ radically in hemipenial structure which, coupled with size-difference in this area might well preclude interbreeding. This being so, it seems reasonable to regard *maculatus* as specifically distinct from *pardalis*, although it cannot be ruled out that connecting populations may yet be found in north Libya with intermediate hemipenes. Typical *bedriagai* and the similar west Moroccan population are tentatively regarded as conspecific with *pardalis* as they are hemipenially similar and the differences between them are mainly in features showing substantial variation within each population. On hemipenial evidence, the Tamesmida population may be specifically distinct from *A. bedriagai* but it seems safest to leave its status undecided until more is known about it.

### The *A. scutellatus* group

*A. scutellatus* (Audouin, 1829): North Africa south to Senegal, Mauretania, Mali, Niger, N. Chad and N. Sudan; S. Israel, N. Arabia, S. and central Iraq.

*A. longipes* Boulenger, 1918a: North Africa including parts of S. Morocco, Algeria, Libya, Mauretania, Mali, Niger and Chad.



*A. aureus* Günther, 1903; Coasatal areas of NW. Africa from S. Morocco to Mauretania; also some neighbouring inland areas.

The *A. scutellatus* group is largely associated with soft-sand habitats (Anderson, 1898; Doumergue, 1901; Flower, 1933; Mosauer, 1934; Gauthier, 1967; Blanc, 1980; field labels on BM(NH) material); this is also suggested by the extensive pectination usually present on the toes. However occasional populations are found on harder substrates (Scortecci, 1946). In north Africa the group occupies many desert areas and, unlike *A. boskianus* in this region, is not largely confined to relatively mesic enclaves. *A. scutellatus* and its relatives have few features plesiomorphic within *Acanthodactylus* but many apomorphic ones including the following: premaxilla often with only five teeth and abruptly narrowed, usual number of presacral vertebrae 23 or 24 with very little sexual variation, fifth sternal rib interrupted in a high proportion of individuals; medial lobe of hemipenis, medial branch of sulcus and medial side of armature absent or greatly reduced, clavula with a  $\cap$ -shaped cross section; subocular scale separated from mouth, five or six upper labial scales anterior to centre of eye (four in *A. aureus*), (10)12–18 ventral scales in longest row across belly; ventrals tessellated, four longitudinal rows of scales on fingers, pectination on digits usually strong; young often uniform above.

The populations that constitute the *A. scutellatus* group show great variation in some features: maximum adult size ranges from about 50 mm from snout to vent to nearly 80 mm, dorsal scales may be coarse and keeled or fine and smooth, transverse counts at mid-body ranging from 36 to 100, number and degree of tessellation of ventral scales varies as does amount of pectination on digits and dorsal pattern ranges from stripes or rows of spots to reticulation or uniformity. From analogy with other species in the genus, keeled dorsal scales, low scale counts, reduced ventral tessellation, limited pectination and striped patterns are all likely to be associated with habitats that have harder substrates and more extensive vegetation, whereas contrasting conditions may be typical of soft, open sand.

Although the *A. scutellatus* group is easily defined, recognition of taxa within it is difficult. Boulenger, (1918a, 1921) treated it as a single species with six varieties. Bons & Girot (1962) pointed out that, as some of these were sympatric, they could not be regarded as mere subspecies and suggested the following arrangement for Boulenger's taxa; they also included a form named by Haas (1957) and another described by themselves.

- A. scutellatus scutellatus* (Audouin, 1829): Egypt, Israel, Sudan.
- A. scutellatus hardyi* Haas, 1957: Arabia, S. Iraq.
- A. scutellatus audouini* Boulenger, 1918a: S. Egypt, Libya, S. Tunisia, S. Algeria.
- A. longipes longipes* Boulenger, 1918a: S. Libya, Algerian Sahara.
- A. longipes panousei* Bons & Girot, 1962: SE. Morocco.
- A. inornatus inornatus* (Gray, 1838): N. Libya, Tunisia, N. Algeria, S. Morocco.
- A. inornatus aureus* Günther, 1903: Atlantic coast from S. Morocco to Port Etienne.
- A. dumerilii* (Milne-Edwardes, 1829): Senegal, Mauretania, Niger.

But this system too presents problems for there is no real evidence that *A. scutellatus*, *A. inornatus* and *A. dumerilii* act as good species, nor is it clear that *A. i. inornatus* and *A. i. aureus* are conspecific. Difficulties in the interpretation of the *A. scutellatus* group arise partly because intrapopulational variation is great and there are large areas in its huge range where material is unavailable. Problems also stem from the geographical structure of the group. The soft-sand habitats favoured by these lizards are by no means continuous and consist of a series of isolates and semi-isolates which have almost certainly had a complicated history of contraction and expansion, and contact and isolation (see, for instance Sarnthein, 1978). The lizard populations associated with these different, partly discrete habitat units are likely to have been subjected to differing selective regimes and even neighbouring populations may show differences. However, although the *A. scutellatus* group exhibits great

variation, it is mainly in a few characters that are likely to be ecologically correlated and it seems possible that similar morphotypes may have developed independently in some cases.

Sometimes, populations may have evolved differences while isolated that enable them to act as good species if contact is restored. Such areas of sympatry or parapatry would provide the best evidence of speciation within the *A. scutellatus* group but, in the stringent environments inhabited by these lizards, the niche space they usually occupy may often be able to support only one species, so that areas of extensive sympatry may be uncommon and regions of contact will frequently be very restricted. Given the poor sampling available, places where two species occur together will not be very easy to find. Nevertheless they do exist and there are others where quite different populations approach each other very closely. On the basis of such localities, the *A. scutellatus* group is best divided into three species *A. scutellatus*, *A. longipipes* and *A. aureus*.

### *A. scutellatus*

As understood here, this widespread species consists of populations in which there are typically less than 70 dorsal scales in a transverse row at mid-body and not usually more than 14 ventral scales in the longest row across the belly (exceptions to both frequent in Egypt and neighbouring areas), five or six upper labial scales anterior to the centre of the eye, premaxilla typically with five teeth, most usually 24 presacral vertebrae and dorsal coloration highly variable. Variation is summarized in Table 5. The name *A. scutellatus* was originally applied to the often large, frequently reticulated, fine scaled populations of northern Egypt. The var. *audouini* of Boulenger is said to differ in usually having spots or vermiculations and in its coarser, keeled dorsal scales but individuals assignable to these two forms occur in the region of Wadi Halfa, Sudan, alongside intermediates and animals from Kufra cannot be convincingly assigned to one form or the other. Other examples attributed by Boulenger to var. *audouini* occur on the coast of Tripolitania but extensive material now in the British Museum (Natural History) shows that these intergrade with other samples assignable to the small var. *inornatus*. The snout-length difference between these forms mentioned by Boulenger is very difficult to demonstrate and is complicated by allometric changes. It seems very improbable, on present evidence, that two species are represented by these samples.

Animals from Mauretania and Senegal were assigned by Boulenger to var. *dumerilii*, regarded as a full species by Bons and Girot. This form is characterized by usually small size, coarse dorsal scales, low ventral number and sometimes striped dorsal patterns. But, if samples are compared, there is a gradual change from south to north the numbers of dorsals and ventrals increasing and striping disappearing (Table 5, localities N–J). The most northern animals are extremely similar to the next available samples in northern Algeria and there are certainly no differences that would suggest they are not conspecific.

In summary, the forms *scutellatus*, *audouini*, *inornatus* and *dumerilii* are not discrete and, on present evidence, cannot be separated at the species level. The pattern of geographical variation in *A. scutellatus* seems too complex to assign subspecies names in any consistent way, at least at present.

### *A. longipipes*

This species can be distinguished from sympatric or parapatric *A. scutellatus* by its higher mid-dorsal transverse scale count (usually over 70 and always over 65), typically greater number of ventral scales in the longest row across the belly (often more than 14) and frequently lower presacral vertebral count (usually 23); the dorsum is typically very pale, either plain or with a reticulation on the flanks. These differences, together with its usually greater pectination on the toes, suggest that it occupies softer, more open sand than *A. scutellatus*, where they occur together. A number of contact or approach areas are known. In northern Algeria, there may be considerable geographical overlap but in Mauretania only a narrow abutment seems to be present with *A. scutellatus* in the west and *A. longipipes* in the

**Table 5** *Acanthodactylus scutellatus*: geographical variation. Locality letters refer to Fig. 8.

	n	Dorsal scales in transverse row at mid-body	Ventral scales in longest row across belly	Known maximum length, snout to vent (mm)	Strength of keeling on dorsal scales (0=none, 4=strong)	Usual dorsal pattern (r-reticulation, p-plain v-vermiculation, s-spots, st-longitudinal streaks)
		10	12	14	16	
A. Arabia	51	46-61	12	21	1	r,v
B. North Egypt	33	64-80	1	30	2	r(occasionally v or s)
C. Jalo, Libya	2	65-70		2		v
D. North Cyrenaica	13	50-61	2	8		often r
E. Inland West Libya	20	55-66		19	1	r,v
F. Coastal Tripoli, Tunisia	64	50-62	8	10		♂♂ often v or s or weak r
G. North Algeria	68	40-65	4	64	4	♀♀ p or s
H. Central Algeria	3	66-67		2	1	♂♂ s or weak r, ♀♀ p or s
I. Fort Gouraud	18	56-66	12	6		v or p
J. K. Atar	56	43-58	1	12	3	♂♂ r or s, ♀♀ s in lines
K. L. Akjoujt	12	44-57		10	2	s
L. M. Nouakchott	23	40-52		17	2	s or st
M. N. Senegal	20	36-47		20		s, r or st
P. Mali, Niger, NW Chad	11	51-63		11		r or st
Q. Kufra	10	60-73		7	1	v or s
R. SW Egypt, Sudan	24	54-73	1	13		♂♂ v, ♀♀ s r, v or s



**Table 6** *Acanthodactylus longipes*: geographical variation. Locality numbers refer to Fig. 8.

	<i>A. longipes</i>				Nearest <i>A. scutellatus</i> populations			
	Dorsal scales in transverse row at mid-body		Ventral scales in longest row across belly		Dorsal scales in transverse row at mid-body		Ventral scales in longest row across belly	
	n		14	16	18	Known maximum length from snout to vent (mm)	12	14
N. ALGERIA,								
MOROCCO								
1. Tuggurt	1	65	1		22-23	60 Tuggurt	1	3
2. Ouargla	4	75-80	4		24-29	62 Ouargla	6	52
3. Kerzaz	3	81-86	2	1	19-23	59 Ain Sefra	10	2
4. Erg Chebbi,								
Morocco (Bons & Girot, 1962)	4	73-80	1	3	18-23	53 Ain Sefra	10	2
MAURETANIA,								
N. MALI								
5. Chinguetti	4	70-80	1	2	1	53 Chinguetti	3	1
6-10. Other localities	8	77-97	1	4	1	61 Chinguetti, E. Mali	7	64
11. NIGER	1	77	1		22	20N 8.40E 53	1	59
SW. LIBYA								
12, 13. Zouarke, Merzouk	3	69-80	2		23-25	55 Merzouk	1	
'Race B' (Scortecci, 1946)		72-92	+	+	18-26	56 'Race A'	(+) +	63
14. N. CHAD	3	70-82	2	1	19-21	55 Zouarke	1	48

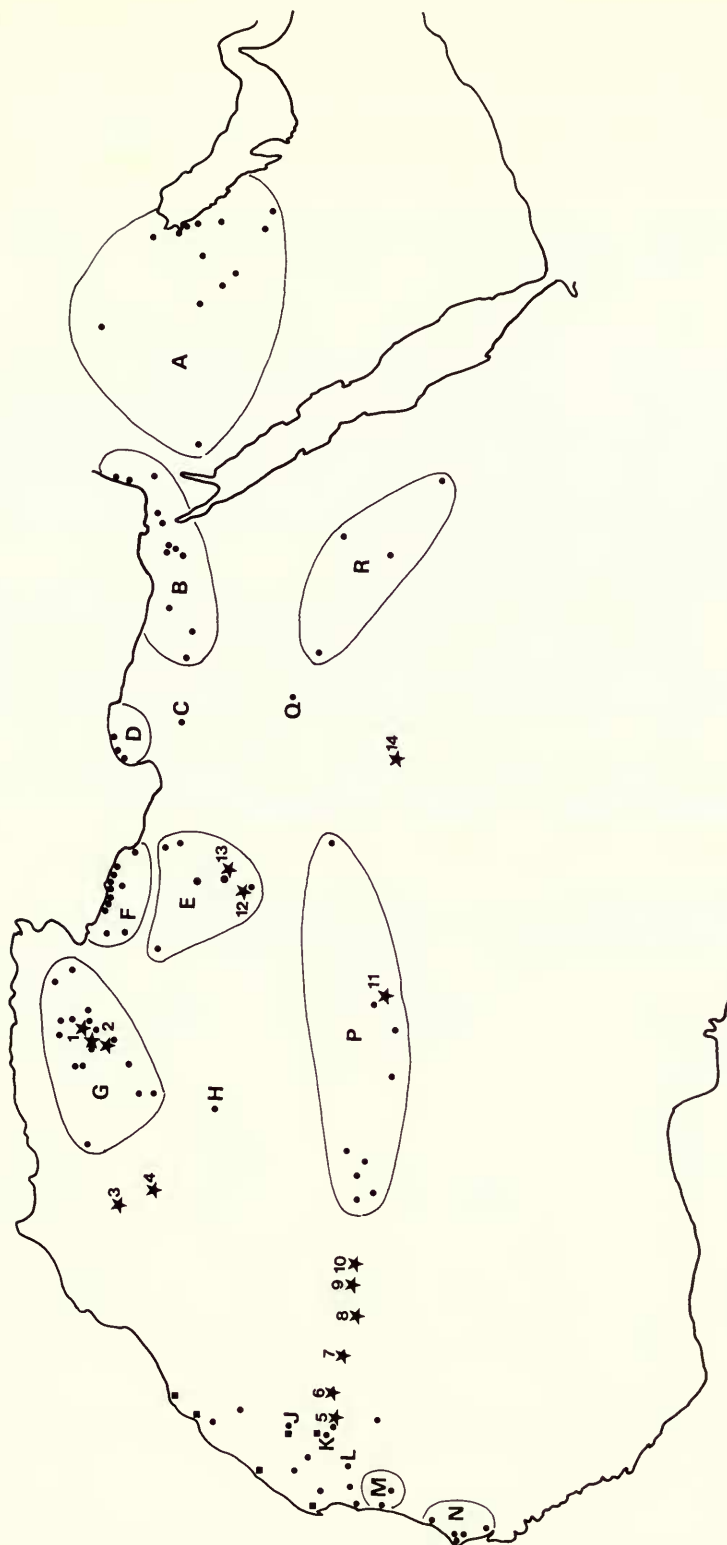


Fig. 8 Distribution of the *A. scutellatus* group based largely on material in the British Museum. ●—*A. scutellatus*; ★—*A. longipes*; ■—*A. aureus*. Letters, for groups of *A. scutellatus* localities defined by thin lines, and figures for individual *A. longipes* localities refer to Tables 5 and 6.

east. In south Libya sympatry may be quite extensive, as indicated by Scortecci, 1946 (his group A is apparently *A. scutellatus* and group B is *A. longipes*). This author's observations give some support to the ecological separation between the two species suggested above.

Localities for *A. longipes* are very scattered and, given the disjunct nature of the sort of habitat that it occupies, this species may consist of several quite isolated populations.

### *A. aureus*

The populations found along the Atlantic coast of northwest Africa are all rather similar and in many respects resemble neighbouring *A. scutellatus* (referred by Bons and Girot to *A. i. inornatus*). They differ most obviously from this species in having only four upper labial scales anterior to the centre of the eye, seven teeth in the premaxilla and the snout is often more acuminate. Such animals, typical of *A. aureus*, may occur some way from the coast (e.g. at Uedi Taamia, 26.01N 13.12W; EBD 2450) but at present they are not known to contact *A. scutellatus*. However, at two localities in Mauretania, the latter occurs alongside another form that may well be conspecific with *A. aureus*. If so this provides some evidence that the latter is a good species. The animals concerned are from Fort Gouraud (♂♂, BM(NH) 1982.292–93) and Atar (♀, BM(NH) 1982.294) and are compared with sympatric *A. scutellatus* in Table 7. They are very similar to typical *A. aureus* in most features and it seems likely that they are referable to this species.

The inter-relationships of the three species that make up the *A. scutellatus* group are unclear. A priori, *A. aureus* might be considered the most primitive, often having seven premaxillary teeth and four upper labials anterior to the centre of the eye. But, if the Mauretanian specimens with five premaxillary teeth are assignable to *A. aureus*, this apomorphic feature cannot be used to unite *A. scutellatus* and *A. longipes* as sister species. Also, the presence of four, instead of five or six upper labials, may be secondary, for other species with acuminate snouts (*A. gongrorhynchatus*, *A. masirae*) have lower labial scale counts than expected from their phylogenetic relationships judged by other features.

**Table 7** *A. aureus*: comparison of samples with neighbouring *A. scutellatus*

	Fort Gouraud, Atar <i>scutellatus</i>	<i>aureus</i>	Coastal area <i>aureus</i>
Upper labial scales anterior to centre of eye	5 or 6	4	4
Dorsal scales across mid-body	45–56	38–46	41–60
Lower temporal scales	large, often keeled	large, smooth	usually small, smooth
Enlarged gular scales bordering 4th and 5th chin shields	frequent	none	rare
Usual number of rows of granules beneath centre of collar	2 or 3	0	0 or 1
Usual number of premaxillary teeth	5	5	7
Pattern of males	Fine spots or reticulation	coarse spots	coarse spots or vermiculation



### The *A. opheodurus* group

*A. opheodurus* Arnold, 1980b: Arabia (but not apparently the southern desert or northern Oman), S. Israel, Jordan, parts of Iraq.

*A. felcis* Arnold, 1980b: S. Arabia (Republic of South Yemen and Dhofar, S. Oman)

*A. masirae* Arnold, 1980b: S. Oman.

This assemblage consists of three small species, all wholly or largely confined to Arabia. All have only recently been described for, although *A. opheodurus* and *A. felcis* have been present in museum collections for some time, they have been confused with *A. boskianus*. These lizards appear to be associated with relatively hard substrates and have restricted pectination on the digits.

The group possesses a high proportion of plesiomorphic features: premaxilla with about seven teeth and not abruptly narrowed (except in *A. masirae*), usually 24 presacral vertebrae in males and 25 in females, fifth sternal rib usually intact; lateral clavula simple, hemipenial connectors unthickened; first supraocular more or less intact, typically four upper labial scales anterior to the centre of the eye, eight or ten ventral scales in longest row across belly, ventrals arranged in straight longitudinal rows, three longitudinal rows of scales around fingers (a fourth row in *A. masirae*), pectination on digits not strong, upper caudal scales keeled, young striped dorsally, the stripes sometimes persisting in adults. However the hemipenis is highly modified in the *A. opheodurus* group, the medial lobe and medial side of the armature being greatly reduced, the fourth supraocular scale is at least partly broken up and the subocular scale is often separated from the mouth (not in *A. masirae*) and the number of stripes in the juvenile pattern shows some reduction. Dorsal scaling is relatively coarse, there being 25–42 scales in a transverse row across the mid-body.

The three species are grouped together largely on the grounds of overall similarity.

### Inter-relationship of the species of *Acanthodactylus*

The approach used for estimating the phylogeny of the species of *Acanthodactylus* is briefly discussed on p. 293. Probably derived character states shared by two or more species (provisional synapomorphies) are listed in Table 8 and their distribution shown in Table 9. Polarity, that is which state of a character is primitive and which state or states derived, has been decided largely by outgroup comparison, using the rest of the Lacertidae as the outgroup. Some assessment of the relative reliability of characters as indicators of relationship (character weighting) was attempted employing the indicators mentioned by Arnold (1981a). No features scored very well on this basis and most scored quite badly but among the better ones were the following (numbers refer to Tables 8 & 9, and Fig. 9): premaxillary teeth reduced to five (1); hemipenial features not thought to be connected directly with the development of physical isolating mechanisms against interbreeding discussed on p. 304 (9, 11–17); reduction in size of the ear opening (24); no keeling on proximal dorsal caudal scales (30). These features are consequently given some precedence in situations where the evidence of different derived character states conflicts. Because many features are polymorphic, with both the primitive and a derived state occurring together in the same species, Le Quesne's (1969) method for determining compatible characters could not be used. As well as joint possession of derived character states, strong overall resemblance is also taken as *prima facie* evidence of close relationship. Using these indicators, a provisional partial phylogeny of *Acanthodactylus* was constructed and is shown in Fig. 9.

The relationships of the *A. cantoris* group, *A. gongrorhynchatus* and *A. haasi* are discussed on p. 311. By and large, the hypothesis of their relationships shown in Fig. 9 involves a pattern of shared apomorphies that does not include much homoplasy. As stated, the main conflict involves the position of *A. schmidtii*: is it more closely related to *A. arabicus* or to *A. blanfordii*? The former relationship is supported by total loss of the medial side of the hemipenis and armature (8d, 10c) and some increase in the number of ventral scales (26b),

**Table 8** Probable derived character states shared by two or more species of *Acanthodactylus*. Where features appear to constitute a transformation series, they are listed in their supposed order of origin and denoted by a consecutive letter thus: a, b, c, d.

1. Premaxilla narrowed: a. somewhat; b. distinctly.
2. Premaxillary teeth reduced to five.
3. Presacral vertebrae 23 or 24 in females.
4. Presacral vertebrae 26 or 27 in females.
5. On average, females have less than one more presacral vertebra than males: a. 0.66–0.84 more vertebrae; b. 0.07–0.33 more vertebrae.
6. Fifth sternal rib interrupted in over 50% of individuals.
7. Hemipenis small.
8. Medial lobe of hemipenis reduced: a. somewhat reduced; b. more strongly reduced; c. very small; d. minute or absent.
9. Proximal lip of medial branch of hemipenial sulcus reduced to a fold in symmetrical hemipenes.
10. Medial side of armature reduced: a. somewhat reduced; b. more strongly reduced; c. reduced to a thread or absent.
11. Medial clavula narrow and pointed with a  $\infty$ -shaped cross section.
12. Lateral clavula with a proximally directed pocket.
13. Lateral clavula very narrow.
14. Lateral clavula complexly structured with multiple lobes below.
15. Lateral clavula complexly structured and divided at tip.
16. Lateral clavula folded with  $\supset$ -shaped cross section.
17. Most medial connector on lateral side of hemipenis thickened.
18. Nostril separated from first upper labial scale by a subnasal.
19. Frontonasal scale longitudinally divided.
20. One or two azygos scales present between the prefrontal scales.
21. Supraocular scales not all intact: a. an area of granules wedged between the third and fourth supraoculars and the latter sometimes divided; b. first supraocular divided into two or three, fourth supraocular very fragmented; c. first and fourth supraoculars very fragmented; d. first, second and fourth supraoculars very fragmented.
22. Subocular scale usually separated from mouth.
23. Upper labial scales anterior to centre of eye more than four.
24. Ear opening reduced in size.
25. Dorsolateral tracts of enlarged scales on posterior body.
26. Maximum number of ventral scales in a transverse row: a. 12; b. 14 or more.
27. Ventral scales tessellated: a. at sides only; b. generally.
28. Ventral scales grade into dorsals: a. to a small extent; b. more generally.
29. Four longitudinal rows of scales on the fingers: a. anterior row irregular; b. anterior row regular and continuous.
30. No keeling on proximal dorsal caudal scales.
31. Tail less than 1.5 times snout-vent distance.
32. Occipital stripes fuse to form a mid-dorsal band (often not visible in adults): a. fusion does not extend to occiput; b. fusion extends to occiput.
33. Young without pattern of light and dark stripes.
34. Reddish-brown spots present in pattern that do not fade in alcohol.
35. Two rows of large ocellar markings along back.

while affinity to *A. blanfordii* is suggested by similarity in lateral clavula structure (12) and the presence of dorsolateral tracts of enlarged scales (25). The former characters appear weaker indicators of relationship, especially as they have developed several times in the Lacertidae, while characters 12 and 25 are known nowhere else. *A. schmidtii* is consequently regarded as the sister species of *A. blanfordii*. Whether *A. haasi* is the sister species of *A. gongrorhynchatus*, which is suggested by its slender habitus, reduced ear opening (24) and some features of the lateral clavula (p. 306), or a hybrid between this species and another such as *A. opheodurus*, is discussed elsewhere (p. 314).





Table 9 continued

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>A. micropholis</i>	-	b	-(a)	(-),a	-	-	-	-	-	-(a)	-	-	-	-	-	-
<i>A. cantoris</i>	-(a)	a	a	(-),a	-	-	a,(b)	-	-	(a),b	-	-	-	-	-	-
<i>A. blanfordii</i>	-	a	a	a	-	-(a)	a,(b)	a	-	b	-	-	-	-	-	-
<i>A. schmidtii</i>	-	a	a	a	-	b	b	a	-	b	-	-	-	a	-	-
<i>A. arabicus</i>	-	a	a	a	-	-	(a),b	a	a	b	-	-	-	-	-	-
<i>A. gongrorhynchatus</i>	-	a	a	-	a	-	a	a	b	b	-	-	-	-	-	-
<i>A. haasi</i>	-	a	a	a	a	-	a	-	b	b	-	-	-	-	-	-
<i>A. schreiberi</i>	-(a)	-	a	-(a)	-	-	-	-	-	-	-	-	-(a)	-	-	-
<i>A. boskianus</i>	-(a)	-a	(-),a	-(a)	-	-	-(a)	-	-	-	-	-	-(a),b	-	-	-
<i>A. grandis</i>	-(a)	-	a	-(a)	-	-	b	b	-	b	-	-	-	-	-	-
<i>A. (t.) tristrami</i>	-	c	-	-	-	-	-	-	-	-	a	a	-	?	-	a
<i>A. (t.) orientalis</i>	-	c	-	-	-	-	-	-	-	-	a	a	-	?	-	a
<i>A. robustus</i>	-	c	a	-	-	-	(-),a	-	-	a	a	a	-	?	-	a
<i>A. erythrurus</i>	-a	c	-a	-(a)	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. savignyi</i>	(-),a	c	-a	-	-	-	-(a)	-	-	-	-	-	-	-	-	-
<i>A. boueti</i>	a	d	-	-(a)	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. guineensis</i>	-(a)	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. pardalis pardalis</i>	-	b	(-),a	(-),a	-	-	a,(b)	-	-	-	-	-	-(a)	-	-	a
<i>A. pardalis bedriagae</i>	-	b	(-),a	(-),a	-	-	a,b	-	-	-	-	-	-	-	-	-
<i>A. maculatus</i>	-	b	(-),a	-a	-	-	a,(b)	-	-	-	-	-	-	-	-	a
<i>A. spinicauda</i>	-	b	(-),a	-	-	-	a	-	-	-	-	-	-	-	-	-
<i>A. aureus</i>	-	a	a	-(a)	-	-	(a),b	b	-	b	-	-	-	-	-	-
<i>A. scutellatus</i>	-	a	a	(-),a	-	-	(-),a,b	a,b	-	b	-	-	-(a),b	-	-	-
<i>A. longipes</i>	-	a	a	a	-	-	b	b	-	b	-	-	-	a	-	-
<i>A. opheodurus</i>	-	a	(-),a	-(a)	-	-	-(a)	-	-	-(a)	-	-	(a),b	-	-	-
<i>A. felcis</i>	-	a	a	-	-	-	-	-	-	-	-	-	-(a)	-	-	-
<i>A. masirae</i>	-	a	-	-	-	-	-	-	-	a,b	-	-	-(a)	-	-	-

- indicates primitive states; a indicates derived features; a, b, c... indicate successive states in a transformation series; no entry indicates that the character cannot be scored; brackets indicate that the state concerned is uncommon.

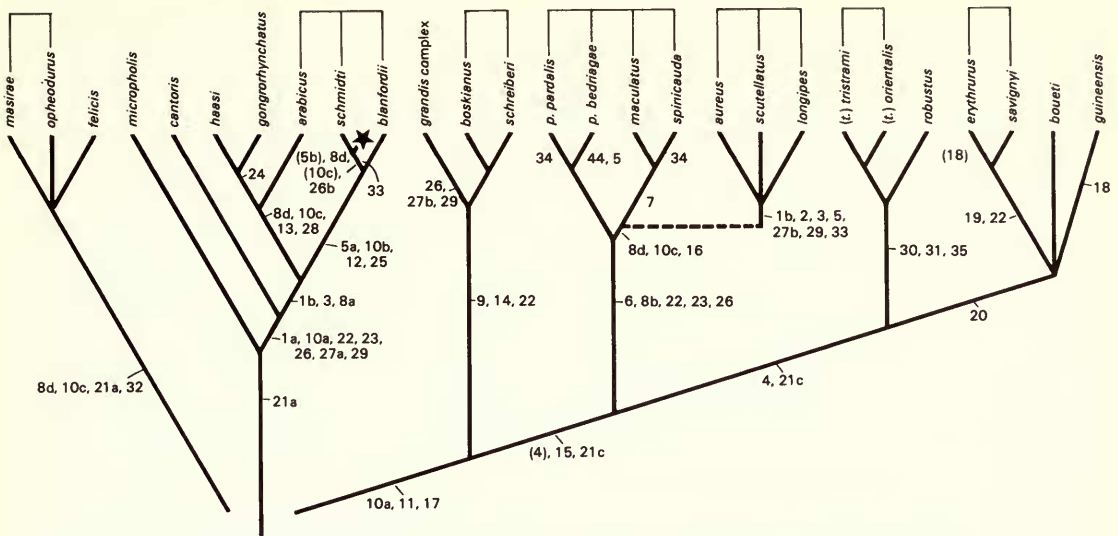


Fig. 9 Tentative hypothesis of the relationships of the species of *Acanthodactylus*. Figures refer to derived characters listed in Tables 8 and 9. Lines above species names join forms that have a very close overall resemblance. ★-indicates alternative position for the *A. scutellatus* group (*A. aureus*, *A. scutellatus* and *A. longipes*).

A number of *Acanthodactylus* species share a distinctive hemipenial structure which incorporates two derived features not found elsewhere: the medial clavula is narrow and pointed with a  $\epsilon$ -shaped cross section (11) and the most medial connector on the lateral side is often thickened (17); in addition there is moderate asymmetry of the armature (10a). This pattern occurs in *A. boskianus*, *A. schreiberi*, the *A. grandis* complex, *A. (t.) tristrami*, *A. (t.) orientalis*, *A. robustus*, *A. erythrurus*, *A. savignyi*, *A. boueti* and *A. pardalis*. It seems probable that these forms constitute a monophyletic group in Ashlock's (1974) sense within *Acanthodactylus*. Among them *A. boskianus*, *A. schreiberi* and the *A. grandis* complex all have a reduced proximal lip to the medial branch of the hemipenial sulcus (9) and a lateral clavula that is complexly lobed (14). Within this trio, *A. boskianus* and *A. schreiberi* may well be sister species, for some populations are extremely similar. *A. grandis* shows conflict of evidence as to its relationships. It has some similarity in derived features to members of the *A. cantoris* group, viz. high number of ventral scales (26) which are tessellated (27b) and four longitudinal rows of scales along the fingers (29b). However, weighting criteria (especially frequent occurrence in groups not closely related to *Acanthodactylus*) suggest these features are relatively weak indicators of relationship, whereas it has been argued (p. 329) that most of the conflicting hemipenial features (9, 11, 14, 17) that ally the *A. grandis* complex to *A. boskianus* and *A. schreiberi* are likely to be of greater reliability. Moreover, any detailed placement of the *A. grandis* complex in the *A. cantoris* group would involve additional homoplasies.

Members of the *A. tristrami* group share features not found elsewhere in the genus, viz. no keeling on the proximal, dorsal caudal scales (30), a short tail (31) and an often distinctive pattern (35). The very similar *A. (t.) tristrami* and *A. (t.) orientalis* could well be sister species. *A. robustus* has some features that suggest relationships elsewhere: subocular scale separated from the mouth (22), increased number of ventrals (26a) and an irregular fourth scale row on the fingers (29a), but none of these derived states is very strongly developed and all seem likely to be relatively weak indicators of relationship compared with those allying *A. robustus* with *A. (t.) tristrami* and *A. (t.) orientalis*.

The *A. tristrami* and *A. erythrurus* groups share some distinctive features, in particular a high number of presacral vertebrae (4) and fragmented first and fourth supraocular scales

(21c). Furthermore, some species of each have a lateral clavula that is bifurcate at its tip (15), so it seems reasonable to regard the two assemblages as closely related. The members of the *A. erythrurus* group are all generally similar and at least some individuals of all species have one or more azygos shields between the prefrontal scales (20) although this condition also occurs occasionally in other forms. It is suggested that *A. erythrurus* and *A. savignyi* are sister species on the evidence of their great similarity and frequent division of the frontonasal scale (19). They are also the only members of the group in which the subocular scale may be separated from the lip (22). *A. boueti* and *A. guineensis* both have distinctive features of their own (*A. boueti*—nine premaxillary teeth, fragmented parietal scales, small hemipenis (7), supraocular scales very fragmented (21d); *A. guineensis*—very asymmetrical hemipenis and armature (8d, 10c), lateral clavula rolled) but their precise relationships to each other and to *A. erythrurus* and *A. savignyi* are not clear. All *A. guineensis* examined ( $n = 20$ ) have a peculiar arrangement of nasal scales (18) which occurs as a rarity in *A. erythrurus* (p. 296). However, this feature cannot be regarded as strong evidence of the close relationship of these species within the group, for its rarity in *A. erythrurus* raises the possibility that its apparent absence in *A. savignyi* and *A. boueti* may be due to inadequate sampling or to pseudoreversal (Arnold, 1981a).

The *A. pardalis* group seems likely to be a monophyletic assemblage on the basis of the strong overall similarity of its members. They also have more hemipenial asymmetry (8b or 8c) than the species placed in the *A. grandis* complex and the *A. boskianus*, *A. tristrami* and *A. erythrurus* groups, share a high incidence of interruption of the fifth sternal rib (6) and the number of ventral scales is also regularly high (26). The main reason for allying the *A. pardalis* assemblage with these groups is that the species with the least modified hemipenis, *A. pardalis*, has an armature just like the others with derived features 10a, 11 and 17. The absence of these features in the other two species in the *A. pardalis* group, *A. maculatus* and *A. spinicauda*, may be secondary, the result of the development of physical isolating mechanisms (p. 304). The *A. pardalis* group shares with the *A. tristrami* and *A. erythrurus* groups frequent bifurcation of the tip of the lateral clavula (15), some fragmentation of the supraocular scales (21b) and some tendency for high presacral vertebral counts (4). However, the last feature is not universal and the supraoculars are less broken up than in these forms. Because of this, the *A. pardalis* group is tentatively placed as a sister assemblage to them. Within the *A. pardalis* group, *A. maculatus* and *A. spinicauda* may be closely related having strongly asymmetrical hemipenes and armatures (8d, 10c) with the lateral clavula folded sideways (16).

Holophyly of the *A. scutellatus* group is supported by the close similarity of its members and their possession of a unique synapomorphy; premaxillary teeth reduced to five (2). Its members have several other derived features that occur elsewhere and these suggest conflicting hypotheses as to the closest relatives of the group. The main candidates are *A. schmidtii*, particularly the populations in the United Arab Emirates that have little sexual variation in the number of presacral vertebrae, and all or part of the *A. pardalis* group. Derived features that these share with the *A. scutellatus* assemblage are set out in Table 10; the *A. grandis* complex shares a much smaller number, namely 26, 27 and 29. Most derived features, eleven, are shared with *A. schmidtii* populations from the United Arab Emirates and only seven with the *A. pardalis* group of which no more than six occur in any one species. Thus on simple count of shared characters *A. schmidtii* would be considered clearly the more likely sister taxon, but the likely quality of the features as indicators of relationship should also be taken into account. In general, the features shared with *A. schmidtii* seem rather weak as they score badly on the weighting criteria listed by Arnold (1981a). For instance, numbers 3, 5, 6, 8d, 10c, 23, 26, 27, 29 and 33 occur in a number of other lacertid stocks; there are additional functional reasons for thinking 8d and 10c may have evolved more than once (p. 304); if the argument on p. 333 that the *A. grandis* complex is more closely related to the *A. boskianus* group than to the *A. cantoris* assemblage is accepted, then characters 23, 26, 27 and 29 must have evolved twice within *Acanthodactylus* and a third independent origin



**Table 10** Comparison of derived features shared by the *A. scutellatus* group with *A. schmidtii* and the *A. pardalis* group.

	<i>A. schmidtii</i>		<i>A. scutellatus</i> group	<i>A. pardalis</i> group	
	Main range	United Arab Emirates		<i>A. pardalis</i>	<i>A. maculatus</i> <i>A. spinicauda</i>
1b Premaxilla narrow	+	+	+	—	—
3 Presacral vertebrae 23 or 24 in females	—	+	+	—	—
5b Little variation in number of presacral vertebrae	—	+	+	+	—
6 Fifth sternal rib often interrupted	—	—	+	+	+
8 Medial lobe of hemipenis very reduced	+	+	+	—	+
10c Medial side of armature very reduced	+	+	+	—	+
16 Lateral clavula folded to produce a $\cap$ -shaped cross section	—	—	+	—	+
23 High number of upper labials	+	+	+	+	+
26 Increased number of ventrals	+	+	+	+	+
27 Ventrals tessellated, at least at sides	+	+	+	—	—
29 Four scale rows on fingers	+	+	+	—	—
33 Young without stripes Strong pectination on toes	+	+	+, —	—	—

would not seem unlikely; a number of features seem to be functionally related to the problems of living in the open, soft-sand habitats occupied by *A. schmidtii* and the *A. scutellatus* group, this is true of 1b, 3, 29, 33 and strong pectination on the digits; the coercive selective forces likely to produce convergence of these features are discussed in the relevant character descriptions. Finally, two features, 3 and 5, are confined in *A. schmidtii* to a very small part of the geographical range, the United Arab Emirates. The restricted distribution of these characters suggest they may well have developed independently within the species. If so, the number of features to be considered is reduced to nine. On the other hand the relationship of the *A. scutellatus* assemblage to the *A. pardalis* group is supported by an apparently unique hemipenial feature (16) and the high incidence of interrupted sternal ribs, a condition not found elsewhere in the genus. Assessing such conflicting evidence is inevitably difficult but, on balance, the author is inclined to believe that the *A. scutellatus* group is most closely related to the *A. pardalis* assemblage.

As stated, the members of the *A. opheodurus* group are placed together largely on the grounds of overall similarity which is especially marked between *A. opheodurus* and *A. felicis*. Shared derived features are 8d, 10c and in some individuals of each species 32a; none of these are unique to the group. Evidence for the inter-relationship of the species is conflicting: *A. felicis* and *A. opheodurus* share 5a and 22 while the latter species and *A. masirae* share 1 and 29, although 29 occurs only in a reduced form in *A. opheodurus* and only in a minority of individuals.

The lack of strong derived characters makes it difficult to relate the *A. opheodurus* group to other *Acanthodactylus*, but absence of a thickened hemipenial connector (17) suggests that it is not directly related to the *A. grandis*–*A. guineensis* sequence (see Fig. 9). Nor is it clear how this sequence relates to *A. micropholis* and the *A. cantor* assemblage.

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### Addendum

Since this paper was submitted for publication, I have had the opportunity to see the recent article on *Acanthodactylus* by Dr Alfredo Salvador. (1982). In the main, we are in agreement over species boundaries within the genus and a number of the divergencies that exist can be attributed to using different criteria for deciding if allopatric populations merit species status or not, always a rather subjective decision. These and other more important disagreements are briefly considered below.

1. The *A. yemenicus* group of Salvador is the same as the *A. opheodurus* group of Arnold (1980b and this paper) but with the addition of a new taxon, *A. yemenicus*. This form has much in common with *A. felicis*. Unlike the other members of the group, its specific status cannot be confirmed by sympatry, as its range is completely separate from the others. There are considerable differences between the two populations from which *A. yemenicus* has been described, Ta'izz and the Sheikh Osman-Aden area, even although these are only separated by some 130 km.

2. *A. erythrurus* group. Salvador treats *blanci* as a full species rather than a subspecies of *A. savignyi*. Given the differences between this form and typical *savignyi*, this course is not unreasonable.

3. *A. pardalis* group. *A. pardalis*, as understood here, is divided by Salvador into three full species: *A. p. pardalis* becomes monotypic as *A. pardalis*, *A. p. bedriagai* becomes *A. bedriagai* and the Moroccan population related to *bedriagai* becomes *A. busacki* n. sp. These forms overlap in many morphological features.

4. *A. tristrami* sens. lat. Salvador regards *A. tristrami*, in its wide sense, as consisting of two subspecies: *A. t. tristrami*, with which *A. t. orientalis* is synonymized, and *A. t. iracensis*. This contrasts with the arrangement adopted here where *orientalis* is regarded as separable from *tristrami* and *iracensis* is synonymized with *orientalis*. A careful examination of the types of all three forms and of most other available material convinces me that the latter course is more appropriate. *A. t. iracensis* cannot be separated from *orientalis* on the basis of the

features mentioned by Schmidt (1939), namely lower transverse dorsal count, less vivid colour pattern and more sharply pectinate toes; nor does it differ significantly in any of the other features investigated. On the other hand, typical *tristrami* differs from *orientalis*, including *iracensis*, not only in its larger size, more numerous dorsal scales and hemipenial structure, but usually also in its deeper snout with convex upper profile, absence of a denticulation on the anterior edge of the ear and virtual lack of pectination on the toes. In addition, the first supraocular is more fragmented (*tristrami*- $n=10$ , average number of fragments on each side 5.4, range 3–10; *orientalis*- $n=17$ , average number of fragments on each side 2.8, range 1–6).

5. *A. scutellatus* group. Salvador divides *A. scutellatus*, as understood here, into *A. scutellatus* in the east and *A. dumerilii* in the west. The two supposed species are said to approach each other in Mali and Algeria but not to intergrade. I have re-examined the BM(NH) material from Mali that Salvador assigns to *A. scutellatus* and *A. dumerilii* and can find no differences in the features that are said to separate them, namely transverse ventral count, snout shape and number of rows of supraciliary granules. Where *A. scutellatus* and *A. dumerilii* approach each other around the Algerian-Tunisian border, I again find no consistent differences in snout shape as mentioned by Salvador, and although there are average differences in degree of fragmentation of the fourth supraocular scale, there is substantial overlap. I consequently regard the separation of *A. dumerilii* from *A. scutellatus* as unproven.

Salvador divides his *A. dumerilii* into two subspecies: *A. d. dumerilii* in Senegal, southwest Mauretania and Mali and *A. d. exiguus* in Algeria and Morocco. The former is said to have 12 instead of 14 longitudinal rows of ventral scales, two instead of one row of supraciliary granules and longer legs. In material I have examined, I find that two rows of supraciliary granules are often absent in the area where *A. d. dumerilii* is reported and leg length is variable. Furthermore, there is a very large intergrade area between the two subspecies where other characters vary clinally. It scarcely seems worth while naming such poorly defined entities, especially when *A. scutellatus* varies so substantially elsewhere in its large North African range and no subspecies names are assigned.

6. The diagnosis of *Acanthodactylus* given on p. 8 does not fully differentiate the genus from *Meroles* or *Eremias*.

Salvador, A. 1982. A revision of the lizards of the genus *Acanthodactylus* (Sauria: Lacertidae). *Bonn. zool. Monogr.* 16: 1–167.